Proceedings of the

VI International Symposium on Biological Control of Weeds

Edited by E.S. Delfosse

University of British Columbia
Vancouver, B.C., Canada
19–25 August 1984

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Preface

The first five Symposia in this series were held at Delemont, Switzerland (1969), Rome, Italy (1971), Montpellier, France (1973), Gainesville, Florida (1976), and Brisbane, Australia (1980). The VI International Symposium on Biological Control of Weeds was held in Vancouver, British Columbia, Canada, from 19–25 August 1984.

The VI Symposium set new records for attendance (135) and countries represented (16) at these Symposia. The largest previous Symposium totals were for the Brisbane meeting, at which 101 attendees represented 15 countries. This increase reflects the increasing emphasis on biological weed control on a world-wide basis.

There are 28 more papers included in this volume than in the V Symposium *Proceedings*, formerly the largest in the series. Ninety-six papers are included in this volume, in the following chapters: Biological Control Theory (12 papers), Economics of Biological Control of Weeds (5 papers), Plant and Agent Variability (3 papers), Conflict of Interest in Biological Control of Weeds (13 papers), Biological Control of Thistles (10 papers), Biological Control of Aquatic Weeds (11 papers), Biological Control of Weeds with Pathogens (17 papers), Reports (22 papers), and the Poster Session (3 papers). Particularly significant in the above list are the chapters dealing with economics, conflict of interest and thistles, as they have not been covered in such detail in previous Symposia, and the relatively large number of papers in the chapter dealing with plant pathogens, which reflects the increased interest in this very important topic.

The Organizing Committee of P. Harris (General Chairman), J.H. Myers (Local Chairman), J.H. Myers and M. Mackauer (Treasurers), A.K. Watson (program), A.T.S. (Fred) Wilkinson (field trips and entertainment), and M. Maw (registration), arranged a well-organized and well-executed Symposium. The Committee acknowledges the following for their assistance and support: Agriculture Canada, Regina Research Station, for clerical help and financial support; Agriculture Canada, Ottawa, for publication of the *Proceedings*; the British Columbia Ministry of Agriculture and Food, Mr. Harvey Schroeder, Minister, for a grant towards preparation of the *Proceedings* for publication, and Dr. Gordon MacEachern, Deputy Minister, for welcoming comments; the CSIRO Division of Entomology, Canberra, Australia, for help in the preparation of the *Proceedings* for publication; the University of British Columbia for providing facilities, and Dr. Peter Larkin, Associate Vice President, for welcoming comments; the U.B.C. Conference Centre and Ms. Ingrid Pinel for aid in arranging accommodation and entertainment; and financial support from Abbott Laboratories, the Chevron Chemical Company, the Mycogen Corporation, and the UpJohn Company.

These *Proceedings* have been typset almost entirely by Ms. E. Parker, formerly of the CSIRO Division of Entomology, and printed from COMp 80 camera-ready copy generated by the CSIRO Division of Entomology typesetting program, TYPSET, developed by Dr. M. Dallwitz, also of the CSIRO Division of Entomology. The logo for this Symposium was designed by J.H. Myers and drawn by Floe Zitten. The cinnabar moth larva is one of Canada's best known, although not very successful, introduced biological control agents. Tansy ragwort flowers are attractive to bees and provide nectar, but the honey produced contains alkaloids and is therefore of inferior quality. This design was created to depict the conflict of interest which has become an important aspect of modern biological control programs. Mr. J. Green, CSIRO Division of Entomology, printed the Symposium photograph.

My special thanks go to Ms. Parker, who in addition to typesetting the manuscript, provided valuable subediting advice; Dr. B.P. Moore, CSIRO Division of Entomology, who translated some of the abstracts; and Ms. J.A. Delfosse, who helped proofread the papers. Some tables were typeset by Technology Media Services Pty. Ltd., Canberra. Ms. Dodi Archibald, Publications Coordinator, Agriculture Canada, was a cooperative and effective representative of the publisher.

The VII International Symposium on Biological Control of Weeds will be held at Rhodes University, Grahamstown, South Africa, sometime in 1988.

Ernest S. Delfosse, Editor
Canberra, Australia
October 1985

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Chapter One
Biological Control Theory

Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 3-12 (1985)

Biocontrol of Weeds: Bureaucrats, Botanists, Beekeepers and Other Bottlenecks

P. Harris

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Abstract

Seven problems facing biocontrol of weeds are discussed: (1) inoculative biocontrol is a matter of public interest, requiring investigation of both monetary and ecological costs and benefits; but enabling legislation is also necessary; (2) prediction of agent damage needed to achieve control may be determined empirically by clipping; (3) laboratory host tests only measure the ability of the agent to utilize the plant — the opportunity to utilize it in nature and the advantage of doing so, also need to be considered; (4) most fears about biocontrol concern the reduction of species or genetic diversity. In fact, consumer pressure is the reason for diversity and the survival of rare plant species; (5) the probability of serious damage to an endangered plant depends on its distribution pattern; (6) some problems in establishing agents are related to the use of agent host races from other plant taxa. The possibility of increasing the genetic base of the agent is discussed; and (7) the alternative is a more precise identification and collection from the target taxon.

Lutte Biologique Contre les Plantes Nuisibles: Bureaucrates, Botanistes, Apiculteurs et Autres Goulots d'Étranglement

Le rapport traite de sept problèmes liés à la lutte biologique contre les plantes nuisibles: (1) la lutte biologique par inoculation constitue un domaine d'intérêt public dont les avantages et les inconvénients sur les plans économique et écologique doivent faire l'objet de recherches, et exige l'adoption le lois; (2) Il est possible de déterminer empiriquement, par échantillonage le degré de degâts materiels que doivent causer les agents biologiques pour parvenir à enrayer les plantes nuisibles; (3) les essais en laboratoire ne permettent que de déterminer la capacité de l'agent biologique à utiliser la plante. Il faut aussi examiner les possibilités et les avantages d'utiliser les agents biologiques dans la nature; (4) la majorité des préoccupations en matière de lutte biologique concernent la réduction des espèces ou de la diversité génétique. En fait, les pressions exercées par les consommateurs ont permis d'assurer la diversité et la survie des espèces de plantes rares; (5) les risques de perturbations graves à une espèce menacée d'extinction dépendent de sa répartition; (6) en matière d'établissement des agents biologiques, certains problèmes sont suscités par l'utilisation de races d'agents provenant d'hôtes d'autres taxons de plantes. Le rapport traite des possibilités d'élargir la base génétique des agents biologiques; et (7) la solution de rechange consiste à adopter de meilleures méthodes d'identification et de prélèvement des agents des taxons cibles.

Introduction

The recent rapid growth in the interest and use of biocontrol of weeds throughout the world has increased the urgency of a number of persistent problems. Several speakers from other disciplines have been invited to discuss aspects of these problems during the VI International Symposium on Biological Control of Weeds (Delfosse 1985). The purpose of this talk is to set the stage in the hope of increasing the progress towards solution. The seven problems that I think will be the most serious bottlenecks in the near future are as follows: (1) how to determine the public interest regarding a candidate weed; (2) poor predictability of effects on target weeds; (3) difficulty of interpreting screening tests; (4) concerns about effect of agents on plant diversity; (5) how to assess the threat to endangered plant species; (6) use of poorly adapted agent host races; and (7) inadequate taxonomic identification of the target weed.

Public Interest

Inoculative biocontrol must be done as a matter of public interest since the effects cannot be restricted to individual properties. Determination of this interest involves assessing the prospective monetary and ecological costs and benefits of biocontrol before releases are made. Biocontrol is only worthwhile if there is a positive return and if it is better than can be achieved by other means of control. To my mind, it is irresponsible to embark on a program likely to cost $2 million and 20 scientist-years (Harris 1979) without such a study. I would like to interest economists in how this should be done but have been horrified by the cynical attitude of some: with a large enough contract, they will determine whatever I want about the weed. I would rather collect the data myself, since unless I am convinced about the justification of the project, I am not likely to be able to get support for it. The problems are often not as great as they first seem: if the costs are in the order of $2 million (Harris 1979) and the benefits in terms of several hundred million/yr, either figure can be out by several million without affecting the justification for biocontrol. It is necessary to determine the returns from other means of controlling the weed for comparison with biocontrol; for example, I think that the study of Cranston *et al.* (1983) for knapweed in British Columbia is a good model for determining the economics of chemical control.

The political aspects of an inoculative project are often much more difficult to solve than the economic ones. For example, a lady in British Columbia complained that *Chrysolina quadrigemina* (Suffr.) (Coleoptera: Chrysomelidae) beetles had destroyed a stand of *Hypericum perforatum* L. (Clusiaceae) she used for making herbal tea (Wilkinson, pers. comm.). I am not sure that she ever understood that the beetles had done her a favour as the plant is toxic. Public uses of weeds run from occasional and unexpected uses like these to important industries like beekeeping, for which a weed may be a major source of pollen and nectar. All of these people have a justified complaint if their interests are not considered or are dismissed arbitrarily.

The approach that I favour is the preparation of an overview report with a wide enough circulation to uncover any interests that were overlooked. It helps the discussion between opposing interest groups, such as may occur between ranchers and beekeepers, if the losses and benefits are quantified in monetary terms. The reports presently being prepared by us also discuss the proposed agents and screening tests. I would like to see them published as a means of increasing their availability, but they are not suitable for most journals.

Not only is life easier if there is general support for a biocontrol project, but unless there is enabling legislation, it may be necessary that support is unanimous because of the rule of law principle. The rule of law is fundamental to a legal system. The Magna Carta in Britain in 1215 was concerned with the rule of law, as it restricted the King from acting arbitrarily, so that subsequently he required enabling legislation. Australia recently found that if there was no enabling legislation it did not matter if a biocontrol program was in the public interest and had general public support (Cullen and Delfosse 1985). The result was an out-of-court settlement with two graziers and two beekeepers who objected to the biocontrol of *Echium plantagineum* L. (Boraginaceae) (Anon. 1983). I suggest that if you do not already have it, you get enabling legislation for biocontrol of weeds.

Predicting the Effect of Biocontrol Agents

I find that there is a credibility gap when I cannot predict how much damage each agent will do to the weed and how much damage needs to be done to control it. Inundative biocontrol avoids this problem as the rate of application, such as 250 kg/ha of the white amur fish (*Ctenopharyngodon idella* Valenciennes; Cyprinidae) for the control of aquatic weeds (van Zon *et al.* 1978) is determined before it is released for use. Inoculative biocontrol if started from scratch is a 20-year program that normally involves the establishment of several agents before control is achieved. It starts with great optimism but by about the 10th year when one or two agents have been established that feed on the weed without reducing its density, the ranchers or other clients have lost faith and the bureaucrats with the funds are restless. The general feeling is that biocontrol is 'pie in the sky by and by'.

The need is to be able to measure progress towards the target in numerical terms. Plant species vary greatly in the amount of damage that they will tolerate. The general rule is that resistance to harvesting or grazing increases with the ability of the plant to replace its leaves (Hyder 1972). This presumably also applies to flowers and roots if these parts are damaged. For example, Julander (1968) found that the perennial forb *Valeriana edulis* Nutt. (Valerianaceae), a deer fodder plant, tolerated removal of 50% of its herbage for 10 years but declined when 75% of the herbage was removed. *Geranium richardsonii* Fisch. & Trautv. (Geraniaceae), on the other hand, declined under a 50% clipping regime; while the shrub *Holodiscus discolor* Maxim. (Rosaceae) was found by Garrison (1953) to produce more when all the annual production was removed during the winter months than if it was not clipped at all.

If *Valeriana* had been the target for biocontrol, an agent consuming 30% of the herbage would not have controlled it; but I do not think that it should be considered a failure as it has achieved at least half the damage needed for control. Shrubs are often more resistent to damage than are herbaceous plants, so it is not surprising that *Lantana camara* L. (Verbenaceae) was able to survive complete summer defoliation by *Teleonemia scrupulosa* Stål (Hempitera: Tingidae) in Hawaii (Andres and Goeden 1971). Control was finally achieved on sites with less than 100 cm rain/yr by establishing agents that attacked the plant during the winter months. Since the ability of plants to regenerate increases with the availability of moisture, the resistance to biocontrol with high rainfall is understandable. These differences could be quantified through clipping tests.

There are problems extrapolating clipping data obtained from potted plants to the field situation. For example Winder and van Emden (1981) reported that insects grazing on *Lantana tiliaefolia* Cham. were generally more detrimental to the plant than an equivalent loss through clipping; but the two were closely correlated. Bigger problems are the effects of competition from other plants and moisture stress. For example, the effects of selective grazing or clipping on one plant species growing in competition with other species was more detrimental to it than clipping all the vegetation (Norman 1960; Bentley and Whittaker 1979). Thus, the threshold should be obtained by inflicting various degrees of damage to a natural population of the weed. A greater amount of damage will be required for control on sites with a higher than average annual production and less if the weed is already under high environmental stress (Harris 1980*a*).

For annual plants the damage threshold might be determined in terms of seed production; but as with perennials, the threshold will vary with the site. For example, Shirman (1981) determined that on bare soil over 99.9% of *Centaurea diffusa* Lam.

(Compositae) seed would have to be destroyed to achieve control. In knapweed growing with relatively light competition from other species, Roze (1981) determined that the threshold was 94% seed destruction. This is close to the reduction already achieved by the seed-head flies *Urophora affinis* Frauenfeld (Diptera: Tephritidae) and *U. quadrifasciata* (Meig.) on some sites (Harris 1980*b*). Thus either the establishment of another agent or an increase in grass competition might tip the balance in these places.

Some aspects of the damage likely to be done by an agent were discussed by Goeden (1983). Other suggestions are likely to arise from the analysis of past successes and failures that are presently underway. It is particularly important to know how much damage individual agent species have actually inflicted. I hope in this regard that Julian's (1982) catalogue will be kept up to date and that the remarks will quantify the damage (such as 30% to 50% defoliation) rather than give a subjective assessment (such as substantial defoliation).

Interpretation of Screening Tests

The IV and V International Symposia on Biological Control of Weeds had papers relating to the difficulty of interpreting screening tests (Dunn 1978; Andres 1981). As far as I am concerned the problem is getting worse as the result of increasing doubts by the authorities responsible for approving agent releases.

Both insects and pathogens frequently have broader host ranges in the laboratory than they do in the field. The knapweed rust, *Puccinia jaceae* Otth. (Uredinales) produces a resistant type reaction in safflower (*Carthamus tinctorius* L.; Compositae) in the laboratory although it does produce a few viable spores. Some pathologists regarded the resistant reaction together with the absence of any field record from safflower as an indication that the crop was safe. On the other hand, other authorities interpreted the ability to produce spores on safflower as a cause for concern.

The parameters that determine whether an insect species will damage a plant species are: (*a*) its ability; (*b*) the opportunity; and (*c*) the advantage of doing so (Harris 1981). The ability to utilize a plant in the laboratory screening tests does not mean it will attack that plant species in the field unless the other two parameters are also positive. The opportunity of using the plant depends on the host-finding ability of the agent as well as its temporal and spacial coincidence with the plant. The advantages of using a plant species relate to plant abundance, its relative suitability as a food source, its mortality on the plant, and the degree of competition from other phytophages. Lawton and Schroeder (1977) and Strong and Levin (1979) established that the number of insects and pathogen species increased with the log of the area occupied by the plant species. Strong *et al.* (1984) suggested that this relationship is a function of the encounter frequency of phytophages that can utilize it. I prefer the alternative explanation that the number of niches for phytophages is limited by interspecific competition although the absolute number increases with area as a result of habitat diversity and variation in the habitat size required by different species. Moran (1983) reported that South African crops derived from native plants were almost exclusively attacked by native oligophagous and polyphagous insects, while introduced crops were attacked by both native and introduced species. Thus the resistance of native crops to introduced pests may result from competitive displacement, while introduced crops offer niches to both native and introduced pests. In terms of biocontrol of weeds, I suggest that feeding by a candidate agent on a plant in the laboratory is more indicative that it will be utilized in nature if the plant is an introduced crop than if it is a scattered native.

Impact of Control Agents on Plant Diversity

There is apprehension expressed by many ecologists, particularly plant ecologists, about the effects of biocontrol agents on species or genetic diversity. It is obvious that plant consumers have a major bearing on the association formed. The principle that covers the general effect is that organisms increase the diversity at lower trophic levels. Elimination of plant consumers results in the domination of a habitat by one or a few species and a decline in diversity. Indeed, Stanley (1973) suggested that the extremely simple flora of the Precambrium Era was typical of an uncropped community and that the sudden diversity that occurred at the end of the Era resulted from the appearance of consumers.

Certainly weeds introduced without natural enemies tend to exclude the native vegetation from habitats to which they are suited. The establishment of biocontrol agents increases the diversity at the site, although the target weed remains. Canadian examples are *H. perforatum* and *Carduus nutans* L. (Compositae) but there are many others around the world. Fears expressed by Fedorenko and Fraser (1978) that the white amur fish would decrease diversity by eliminating its preferred food plants, mostly desirable natives, before controlling the weed have not materialized (Pierce 1983). Indeed diversity has sometimes increased slightly (van Zon *et al.* 1978). Unfortunately the fish remains banned from Canada.

Table 1. Plant rarity[1] and risks from biocontrol control agents.

Plant	1	2	3	4	5	6	7	8
Frequency	Abundant	Abundant	Abundant	Abundant	Sparse	Sparse	Sparse	Sparse
Range	Large	Large	Restricted	Restricted	Large	Large	Restricted	Restricted
Habitat	Several	Specific	Several	Specific	Several	Specific	Several	Specific

Consequence of damage to plant survival increases from 1–8.
Likelihood of specialized agent achieving damaging populations increases from 8–1.

[1] Adapted from Rabinowitz (1981).

A field study by Brown (1982) on the effects of excluding consumers from an early succession plant association showed that there was a slower accumulation of plant species when consumers were present. Thus, the fears of plant ecologists are not without some basis, but I think that the effects are temporary, resulting from a slower accumulation of plants on bare ground when consumers are present.

Endangered Plant Species

The endangered species act of the U.S.A. prohibits actions that are likely to compromise the survival of an endangered species. This has meant both the biocontrol Review Committees and researchers have tended to shy away from candidate agents that are able to develop on an endangered plant in the laboratory. Rabinowitz (1981) classified plants (Table 1) into eight categories of increasing rareness. These are not equally at risk from a biocontrol agent that will feed on them. The likelihood of damage increases with the abundance, although certainly the consequence of damage for plant survival increases with rareness. Rabinowitz (1981) cites the example of *Aristolochia serpentaria* L. (Aristolochiaceae) in which rareness provides a survival advantage as the plant escapes from its herbivore *Battus philenor* (L.) (Lepidoptera: Papilionidae).

The result is that reproduction is greater so the plant becomes common locally and loses its advantage. A similar relationship has been established for other plants (Ralph 1977) and can commonly be found in biocontrol of weeds. For example, in British Columbia the relative population density of the moth *Tyria jacobaeae* L. (Lepidoptera: Arctiidae) and hence the damage inflicted by it has declined more than its host plant *Senecio jacobaea* L. (Compositae) (Harris *et al.* 1978). Root and Kareiva (1984) reported that the butterfly *Pieris rapae* (L.) (Lepidoptera: Pieridae) is an exception to the normal resource concentration behaviour, because the female flies a distance between each oviposition with the result that in dense collard stands many hosts are overflown. However, I would be surprised if on a regional basis the attack level per plant was not higher where there were many hosts than where there were few. Thus, I have little concern for endangered plants with a sparse distribution unless they meet the following three conditions: (1) they occur in the same region as a common host; (2) they are readily accepted by the agent; and (3) they support good agent survival. Even in these circumstances I am not concerned about plants in category 8 such as *Betula uber* (Ashe) Fernald (Betulaceae). This tree was rediscovered at the original sites 61 years after it was described. It consisted of 12 trees, 1 sapling and 21 seedlings. In a similar situation the only known population of the tree *Hakea pulvinifera* L. Johnson (Proteaceae) in Australia was eradicated by construction of a parking lot (Bell 1983). I think the only hope for such species is the protection of botanical gardens. Rabinowitz (1981) was unable to find any North American plant to fit category 7 so such species may not exist. The plants that I feel are at greatest risk are those in category 4, but even in these species, agent survival must be adequate for it to build up a large population or there is a large migration from a sympatric weed host. Plants targeted for inoculative biocontrol of weeds are normally those in categories 1 and 2.

The danger of a biocontrol agent to a rare plant should not be considered in isolation from other pressures on them. According to Sukopp and Trautman (1981), 89 of the 581 endangered plant species in Germany are in this predicament as the result of herbicide application. Thus, if the biocontrol of a weed is likely to remove the need to treat large areas with herbicides, it may save more rare species than it places at risk. Competition from the target weed may also threaten native species. Bell (1983) suggests that two Australian plants have been exterminated by competition from introduced plants and 50 species are threatened. Again the possible threat of one agent to a rare plant must be balanced against the saving of others.

Individual States and Provinces in North America have tended to compile endangered species lists of their own; however, frequently the plants listed are merely at the edge of their distribution and the species as a whole is not endangered. The result is that there is a confusion of plants that individual botanists think are worthy of protection. Fortunately, the Federal Register (U.S. Dept. Interior 1980) provides a well-researched list of plants endangered in the U.S.A. and with few exceptions, plants not on the list are not endangered on the continent.

Agent Host Races

Many problems with getting an agent established are related to the use of strains from other species or strains of the weed. For example, the thistle head weevil, *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae) consists of a number of host races. Collections from the thistle *C. nutans* in Europe were readily established on this thistle in North America but could not be established on *Silybum marianum* (L.) Gaertner (Compositae) (Goeden 1978). However, strains of the weevil have been established in North America on this thistle as well as on *Onopordum acanthium* L. (Compositae) by release of weevils collected from the target thistle.

Similarly, the rust *Puccinia chondrillina* Bubak & Syd. introduced into Australia is only effective against one form of *Chondrilla juncea* L. (Compositae) (Burdon *et al.* 1981). The specificity of host races is not always revealed in laboratory tests. For example, the spurge hawk moth, *Hyles euphorbiae* L. (Lepidoptera: Sphingidae), develops as readily on leafy spurge (*Euphorbia esula* L.; Euphorbiaceae) as it does on cypress spurge (*E. cyparissias* L.) in feeding tests. However, a stock of the moth obtained from cypress spurge and released on leafy spurge in Ontario in 1973 has not been found on leafy spurge but a large population did appear on cypress spurge 9 km away (Harris 1984).

It is obvious that if possible, importation for release should be from the same plant species and strain on which the release is to be made. According to DeBach (1969), many taxons designated as host races have sufficient genetic stability and isolation to be full species. There is some advantage in raising them to full species to remove confusion. This will require much greater use of biochemical techniques to investigate genetic isolation. For example, electrophoresis can also be used to help identify pathogens licensed for inundative biocontrol (see Feichtenberger *et al.* 1984).

There are some strategies that might be tried if the correct host strain is not available. In mosquitoes positive heterosis has been obtained by crossing strains from different geographical areas (Legner 1972). Also, Seawright *et al.* (1975) and Lorimer *et al.* (1976) obtained beneficial results by crossing inbred laboratory colonies before release. This might be used as a method of overcoming the vigour loss associated with prolonged laboratory propagation. Releases from several sources are presently being made to increase numbers, but not as far as I know to obtain hybrid vigour.

Huettel and Bush (1972) crossed two sibling species of the fly *Procecidochares* (Diptera: Tephritidae) from different host plants. The F_1 generation were laid into the host of the female parent but the back cross of the hybrid flies produced many individuals that readily accepted both hosts. I suggest that this technique might be used for expanding the host range of insects used for the control of *L. camara*. The genetic turmoil in this man-made polyploid species (Spies and Stirton 1982) has resulted in many plants that escape partially or completely from the control agents. Clones of the sterile cactus *Opunita aurantiaca* Lindley (Cactaceae) may present a similar problem. The moth *Tucumania tapiacola* Dyar (Lepidoptera: Pyralidae) survives on the cactus in Australia but died out when released in South Africa (Hoffman 1982). The cactus is a hybrid of disputed parentage (Arnold 1977; Moran and Annecke 1979) but nobody disputes the considerable variation within the species. Regardless whether the failure in South Africa is related to differences in the host plant or to the climate, an increase in the genetic diversity of the moth by crossing stock from different hosts in different regions would be advantageous.

Leonard (1982) suggested that the host range of pathogens introduced for biocontrol should be expanded to cover the variation in the weed population by crossing pathogen isolates with the appropriate genes for virulence. Presumably the capabilities of a control agent can also be increased by genetic engineering but the extent to which society will approve the release of such organisms is still to be determined.

Identification of the Target Weed

There are problems for biocontrol when there are uncertainties about the taxonomy of the target weed and this applies to about half the weeds targeted for biocontrol in

Canada. North American taxonomists do not necessarily follow European usage when classifying plants introduced from Europe. For example, all the knapweeds in the section Maculosae in the *Flora Europeae* that have been introduced to North America are placed in the species *Centaurea maculosa* Lam. (Compositae) (J. McNeill, pers. comm.). In Europe *C. maculosa* is a biennual diploid whereas the problem weed called *C. maculosa* in British Columbia is a perennial tetraploid that seems to be referable to the European *C. bibersteinii* DC. There is also another spotted knapweed in Saskatchewan that is clearly not the same as *C. bibersteinii*, so it is presumably new to the Canadian flora. Similarly, considerable time and effort has been wasted collecting and screening insects from the spurge called *Euphorbia esula* in Europe only to find that they died on the plant called *E. esula* in Canada. According to Radcliffe-Smith (1984), there are five species and three hybrids of spurge in Saskatchewan and 20 in North America that presently go under the name *E. esula*. Other examples are discussed by McNeill (1982). I suggest that the problem is serious enough that before a search is started in Europe for control agents, the weed species should be submitted to European botanists, so regardless of the name, the right plant will be searched.

The problem is more difficult if the weed has changed genetically since its introduction. For example, the man-made polyploid *L. camara* in South Africa consists of diploid to hexaploid forms with chromosome configurations from univalent to heptavalent; the plant is evolving differently in India and South Africa (Spies and Stirton 1982). In this situation I think that the best that can be done is to attempt to broaden the genetic base of the agent.

Test plants used for determination of the host range of an agent are largely selected on the basis of their relationship to the host (Wapshere 1974). This is a problem in the genus *Senecio*. According to Jeffrey *et al.* (1977) the variation range in the genus overlaps and even exceeds that of several other genera. They suggested that the present genus should be divided into three subtribes containing 16 genera. Also, according to Douglas (1982), *Senecio* taxons that are treated as species would be treated as subspecies in other genera of the Asteraceae. No wonder *Senecio* is the largest genus of plants in the world.

I suggest that biocontrol workers may need the help of a sympathetic botanist; but if such a person cannot be found, be wary of authoritative-sounding plant classifications.

Conclusion

Many of the problems that I have touched on will be discussed in more detail by other speakers during the V International Symposium on Biological Control of Weeds. Very likely this will be done from a different perspective so I hope there is a good discussion both at and after the Symposium and assists in reaching solutions. I feel strongly that some of the problems are so serious that unless they can be resolved soon, they will restrict the growth of biocontrol of weeds.

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Ecological Theory and Choice of Biological Control Agents

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Abstract

From many possible topics, three are selected for discussion: the population dynamic characteristics of successful control agents in theory and practice; host shifts and the risks inherent in biological control; and the possibility of using exotic insects to control native weeds. (i) One group of population models proposes that successful control agents show strong aggregative responses to high density host patches. More recent studies cast doubt on this theoretical insight; pertinent field data are virtually non-existent. Whether better understanding of this problem would lead to better practical weed control is a moot point, but it deserves attention. (ii) Worries about biological control agents switching to non-target plants are persistent, but unjustified. Studies on native insect faunas suggest that in general, the probability of an insect used in a biological control programme unexpectedly switching to a non-target host is of order of 1×10^{-8} to 1×10^{-7} insect species, plant species^{-1} year^{-1}. Despite these minute risks, further studies on the genetical, physiological and behavioural changes involved in host shifts would be helpful when selecting biological control agents. (iii) Finally, the use of exotic insects to control native weeds is addressed. Successful application demands detailed theoretical and practical studies on the ecology of native insects feeding on the target weeds. Plans for the biological control of bracken fern, *Pteridium aquilinum*, in Britain are outlined, using exotic, apparently bracken-specific insects from South Africa, selected to occupy vacant niches in the resident British insect community on bracken.

Théorie Écologique et Choix des Agents de Lutte Biologique

Sur un vaste choix de sujets, trois domaines ont été retenus aux fins de l'étude: (1) les caractéristiques de la dynamique des populations des agents biologiques efficaces: théorie et pratique; (ii) la substitution d'hôtes et les risques inhérents à la lutte biologique; (iii) les possibilités d'utilisation d'insectes exotiques pour lutter contre les plantes nuisibles indigènes.

D'après les modèles 'classiques' des populations, pour réussir les agents biologiques doivent être fortement attirés en masse sur les touffes denses des plantes hôtes. Des modèles plus récents remettent cette théorie en question, et il n'existe pratiquement aucune donnée pertinente sur le terrain. Une meilleure compréhension de ce problème permettrait-elle d'arriver à des méthodes plus pratiques de lutte contre les plantes nuisibles? C'est là un sujet à controverse, mais qui mérite plus d'attention.

De temps à autre, on s'inquiète de l'infestation des plantes non-cibles par les agents biologiques. D'après les études théoriques et expérimentales sur la substitution d'hôtes des insectes indigènes, les risques à long terme associés à ce phénomène dans les programmes de lutte biologique modernes n'existent qu'à peine ou pas du tout.

Finalement, l'auter traite de l'utilisation d'insectes exotiques pour la lutte contre les plantes nuisibles indigènes. Pour réussir de telles tentatives, il faut procéder à des études théoriques et pratiques sur les insectes indigènes. Il présente aussi le programme de lutte biologique contre le ptéridium des aigles (*Pteridium aquilinum*) que l'on prévoit mettre en oeuvre en Grande-Bretagne par l'introduction d'insectes exotiques d'Afrique du Sud, dont l'unique hôte est la fougère, et qui ont été choisis pour combler les lacunes de la communauté d'insectes indigènes de Grande-Bretagne qui fréquentent les fougères.

Introduction

Data from biological control programmes have undoubtedly contributed more to theoretical ecology than theoretical ecology has contributed to biological control (see, for example, Beddington *et al.* 1[illegible] [illegible]er and Hall 1982; Caughley and Lawton 1981; Hassell 1978, 1980; Murdoch *et al.* 1984). Reasons for this asymmetry are not hard to find; it is often too expensive, or impossible, to gather information that theoreticians suggest would improve the practice of biological control, or appropriate theory is poor, unconvincing, or absent. Nevertheless, this should not prevent us from trying to improve the practice of biological control by careful use of existing theory (e.g. Harris 1981*a*; Price 1981), or from nurturing the development of more and better theory. An encouraging recent development is the Silwood International Project on the Biological Control of Weeds, a comprehensive theoretical and practical analysis of biological weed control programmes, currently being undertaken by a group of biocontrol workers and ecologists centred on Imperial College and CIBC at Silwood Park in England.

My aims in this paper are considerably more modest than the Silwood Project! Theoretical ecology is a broad church, and from among many possible topics I have selected three for consideration. They are deliberately very different. The first addresses the question of whether successful biological control agents have similar population dynamics, and whether these dynamics account for their success. Section two of the paper then moves to the question of risks in biological weed control, and measures the probability of host shifting to non-target plants by insect control agents. Finally, the problems and possibilities for biological control of a native weed *Pteridium aquilinum* (L.) Kuhn. (bracken fern; Dennstaedtiaceae) in the U.K., using exotic insects are discussed. Between them, these three topics allow discussion of a range of theoretical problems of interest to biological control workers, and highlight places where ecological theory might help in the choice of biological control agents.

Population Dynamics Theory and Selection of Biological Control Agents

The hallmark of successful biological control is a persistent, marked reduction in the pest population. A useful measure of the magnitude of this reduction is:

$$q = N^{*}/K, \tag{1}$$

where q is the ratio of the density of the pest population, N^{*}, in the presence of a controlling agent, divided by the density of the pest, K, prior to control. Estimates of q are available both for insect pests successfully controlled by parasitoids (Beddington *et al.* 1978; Strong *et al.* 1984) and plants controlled by herbivores (Caughley and Lawton 1981; Strong *et al.* 1984).

Interpreting q*-values*

As a basis for developing theoretical understanding, more and better estimates for q in biological weed control programmes would be valuable. However, existing data are sufficient to establish that q-values of order 0.01 or less, are not uncommon. Theoretical interest in low q-values is considerable, because stable q-values less than 0.1 are surprisingly difficult to generate in population models (Beddington *et al.* 1978; Caughley and Lawton 1981; Crawley 1983). The most complete theoretical framework exists for insect host–parasitoid systems, where detailed mathematical models of the interaction (see Beddington *et al.* 1978; Hassell 1978, 1980; Hassell and Waage 1984) suggest that successful biological control of insect pests (i.e. $q \approx 0.01$) by parasitoids hinges on two phenomena: (i) high parasitoid searching efficiency, generating strong host depression; and (ii) a spatially aggregated host population, on which aggregating parasitoids impose spatially density-dependent mortality. It is aggregation by the parasitoids in regions of high host density that generates stability in the interaction, particularly at very low q-values.

Arguing largely by analogy from these host–parasitoid models, Caughley and Lawton (1981) suggested that spatial heterogeneity in the distribution of weed populations, and non-random, spatially density-dependent mortality induced by herbivores may also be crucial for population stability in successful biological weed control. Unfortunately data to test this suggestion are virtually non-existent. Moreover, realistic but tractable models of insect–plant interactions are considerably more difficult to construct than parasitoid–host models (Crawley 1983). Indeed, Crawley's (1983) models imply that herbivore aggregation alone is not sufficient to guarantee a low, stable q. Under some circumstances, *reducing* herbivore aggregation leads to a dramatic reduction in plant abundance, for example when herbivores reproduce on their host, but have rather poor powers of dispersal between hosts (Crawley 1983, pp. 274–7).

Very simply, we do not understand the crucial dynamic processes involved in the successful control of weeds by insect herbivores. Whether such knowledge would itself lead to the selection of better control agents in the future is debatable. For example, it may simply be too expensive, time consuming and difficult to discover whether a potential agent has the 'right' dynamics. However, we cannot judge whether this will be the case until we know whether successful control agents do indeed share a suite of characteristics lacking in unsuccessful species. In passing, note that we are not concerned here with the timing and type of damage inflicted by successful control agents; these may determine levels of host depression (Harris 1981*b*; Schroeder 1983), but not the stability of the interaction. It is no good devastating a weed one year if it flares up again in subsequent years.

Questions About the Population Dynamics of Successful Control Agents

A better understanding of the mechanisms preventing unstable oscillations in biological weed control programmes might emerge from the following.

How are patterns of herbivore attack and host mortality spatially distributed in successful, and equally important, in unsuccessful control programmes? Clumped distributions of herbivore attack are known to occur in some successful cases of control (Caughley and Lawton 1981; Zwölfer and Harris 1984), although patterns may vary with climate and other variables (Zwölfer and Harris 1984). Moreover, the responses of insect herbivores to host plant density and distribution are many, varied and poorly understood (reviews in Kareiva 1983, and Strong *et al.* 1984). Many Lepidoptera, for example, differentially oviposit on isolated rather than clumped hosts. Which patterns of behaviour, if any, are characteristic of good biological control agents?

Unfortunately, measuring spatial patterns of herbivore attack is not straightforward. Patterns may vary with the scale of measurement; i.e. single plants, small groups of plants, patches of a few square metres, etc. (Heads and Lawton 1983). Moreover, insect mortality between the egg and larval stages may mean that patterns of host attack generated by ovipositing adults are not the same as those produced by feeding larvae (e.g. Zwölfer and Harris 1984), adding a further layer of complexity to an already difficult problem.

All this presupposes that spatially density-dependent mortality imposed on the plant population by herbivores is the key to persistent, stable biological control. But alternative theoretical scenarios are possible. For example, spatial refuges, where enemies cannot or do not go, may allow the weed to repeatedly reinvade the rest of its habitat. Outside the refuge, victim and enemy interactions may be unstable (in a formal, population dynamics sense) with frequent local extinctions of both weed and enemy. The woodland refuge for *Hypericum* (Clusiaceae) against *Chrysolina* (Coleoptera: Chrysomelidae) (Huffaker 1964) may be one such example. This particular theoretical scenario, one of repeated local extinctions and reinvasions, appears to be the one favoured by Murdoch *et al.* (1984, 1985) to account for cases of successful biological control of insect pests.

Alternatively, introduced biological control agents may simply depress pest numbers so much that the pest's depleted population becomes susceptible to density-dependent regulation by a second agent, a polyphagous predator (if the pest is an insect) or generalist herbivore, effective at low but not high pest densities (Beddington *et al.* 1978; Hassell 1978; Southwood and Comins 1976; Price 1981). This hypothesis has something of a *deus ex machina* quality about it, but it cannot be ignored simply because it invokes the help of an outside agent to maintain the stability of the interaction. A variant on this hypothesis would be to suggest that steps to improve and restore the habitat by reducing overgrazing (e.g. Goeden and Ricker 1980) are sufficient to prevent the weed from recovering after biological control agents have reduced its population.

Finally, it is possible that one or more of the large number of elements that go to make up a 'typical' plant–herbivore interaction (Crawley 1983) generates stable, density-dependent persistence of the plant and its herbivore control agent at low q-values, but not via the original hypothesis of spatial density dependence. One recent, unexpected discovery in host–parasitoid models is that variable parasitoid sex ratios contribute markedly to the stability of the interaction (Hassell *et al.* 1983). Whether a creative theoretician can discover some equally surprising, stabilising process in the dynamics of insect–plant interactions remains to be seen.

In sum, we do not understand the population dynamics of successful biological weed control. We cannot even hazard a guess as to whether a similar mechanism promotes stability in all successful programmes, or whether each case is unique. Hence, population dynamics theory cannot help us pick better control agents. But as a long-term strategic objective, I believe that this problem deserves more attention.

The Problem of Host Shifts

One of the most frequent worries raised against biological weed control is that it might not be safe; that even after careful and comprehensive screening (CIBC 1978; Schroeder 1983) biological control agents might still eat something else. There are at least two facets to this problem. First, what is the probability of an insect biological control agent making an unexpected host switch? Second, how might ecological theory help us to evaluate starvation screening trials that reveal some ability by proposed control agents to feed on plants other than the target weed?

As Schroeder (1983) points out: 'Biological control of weeds has been practiced for more than 75 years and introductions of control agents have been made against more than 86 weeds in some 20 countries (Julien 1982). In all instances where host range tests ... have been undertaken there have been no adverse or unpredictable results'. Batra (1981) makes much the same point; indeed all biological control workers know that their science has an excellent and enviable safety record, but it may nonetheless help when arguing with legislators and administrators to have a quantitative assessment of risk, to underpin what we all know is true.

The Risk of Unexpected Host Shifts

'Host shift' is a widely used term of convenience. It does not imply that an insect population abandons an old host to take up occupation on a new host species. Rather the new host is simply added to the insect's dietary repetoire. Clearly, the probability of insects shifting hosts is not zero. If it was zero, there would be no host races of one species of insect exploiting different food plants in different geographical regions;

in fact, geographical host races are common (Fox and Morrow 1981; Strong *et al.* 1984; Zwölfer and Harris 1984). Nor would plants accidentally or deliberately introduced into a new region recruit an insect fauna; most introduced plants recruit herbivores surprisingly quickly (Strong *et al.* 1984).

In the present context, we can learn a great deal from insects recruited onto introduced plants. In biological control work, an introduced insect is exposed to a novel flora of native plants and crops, with a small but finite probability that it may unexpectedly shift hosts and attack one or more of these non-target species. Some idea of the magnitude of the risk of this occurring can be gauged from the analogous 'experiment' in which novel (introduced) plants recruit insects from a native fauna. The best data are for insects known to have colonised introduced trees in Britain (Kennedy and Southwood 1984). The pertinent data are: (*a*) the length of time a tree has been present in Britain; (*b*) the number of insect species now feeding on each species of alien tree; and (*c*) the total numbers of herbivorous insects in appropriate taxa in Britain. (When defining the pool of potential colonists, I have made no distinction between herb- and tree-feeders, because many recorded host shifts have been between plants of very different growth forms; e.g. Winter [1974].)

An estimate of the annual probability, or risk, of one species of insect shifting to a novel host, is $b/(a \cdot c)$.

Appropriate data are summarised in Table 1, giving the individual probabilities of host shifts for various insect taxa × tree combinations summarised in Fig. 1, and an overall probability of one insect species shifting onto one new host plant of 3.6×10^{-6}year^{-1}. (A total of 104 documented host shifts, from a pool of 6175 British insects, over 4700 tree-years.)

This is a very small risk, but for biological control agents it is a serious overestimate. Successive corrections to make the risk assessment more realistic are as follows. (i) Most of the insects colonising introduced plants are externally feeding polyphages (Strong *et al.* 1984). Host shifts are rarer, but not unknown amongst oligophages and monophages. Of 103 cases involving colonisation of exotic trees and shrubs in Europe (Strong *et al.* 1984), 10 were by stenophagous insects, normally feeding on native plants in the same genus as the introduced plant; 8 were stenophages from plants in the same family but different genera; 68 were polyphages, attacking plants in more than one family; and 17 were stenophagous insects attacking a narrow range of hosts in a different family to the introduced plant. One may safely assume that screening in biological control programmes would prevent all but the most unexpected shifts, i.e. those in the last category (Schroeder 1983), reducing estimates of apparent risk by a factor of 17/103; i.e. to $0.165 \times (3.6 \times 10^{-6})$ or to 5.9×10^{-7} insect species, plant species^{-1} year^{-1}. (ii) Trees are much larger 'targets' than other plants for colonisation by insects, over both ecological and evolutionary time (Lawton 1983, 1985). In other words, probabilities of host shifts onto trees are enhanced compared with most plants. In general, trees have insect faunas an order of magnitude richer than herbs (Lawton 1983, 1985); if half this difference in faunal richness is simply attributable to their larger size (Lawton 1985) this suggests that general risks of host switching should be half an order of magnitude less than the figure of 5.9×10^{-7}, i.e. risks of host shifting should, in general, be a number of order 1×10^{-7} insect species, plant species^{-1} year^{-1}. (iii) Finally, newly introduced plants are full of vacant niches. Native plants, and well-established crops should in principle be much harder for introduced insects to colonise. A biological control agent may be unable to successfully shift to a non-target host because it is competitively excluded by resident insects. Two mechanisms of exclusion are possible, conventional interspecific competition for limiting resources such as food or oviposition

Table 1. Documented host-shifts by native British insects onto introduced trees, from Kennedy and Southwood (1984). All data in the table are from this study, except as indicated in the footnotes. Although no Agromyzidae, Cecidomyidae, or Thysanoptera have colonised any of the seven species of introduced trees, each of these insect groups has representatives feeding on native trees.

Insect group	Tree Species							Herbivorous insects: total species in British 'pool'
	Acer pseudoplatanus	*Aesculus hippocastanum*	*Castanea sativa*	*Juglans regia*	*Larix decidua*	*Quercus ilex*	*Robinia pseudoacacia*	
Diptera: Agromyzidae	0	0	0	0	0	0	0	313[2]
Diptera: Cecidomyidae	3	0	0	0	1	0	0	622[3]
Hemiptera: Heteroptera	1	0	0	0	3	0	0	283[1]
Homoptera	10	5	1	2	6	1	1	976[1]
Hymenoptera: Symphyta	2	0	0	0	5	0	1	473[3]
Hymenoptera: Cynipoidea	0	0	0	0	0	0	0	118[3]
Lepidoptera	20	2	9	2	16	4	0	2 233[1]
Thysanoptera	0	0	0	0	0	0	0	183[1]
Coleoptera	2	0	1	0	6	0	0	975[1]
Years since tree introduced to Britain	650	400	1 900	600	350	400	400	—

[1] From Price (1980).

[2] From Spencer (1972).

[3] From Kloet and Hincks (1964–1975).

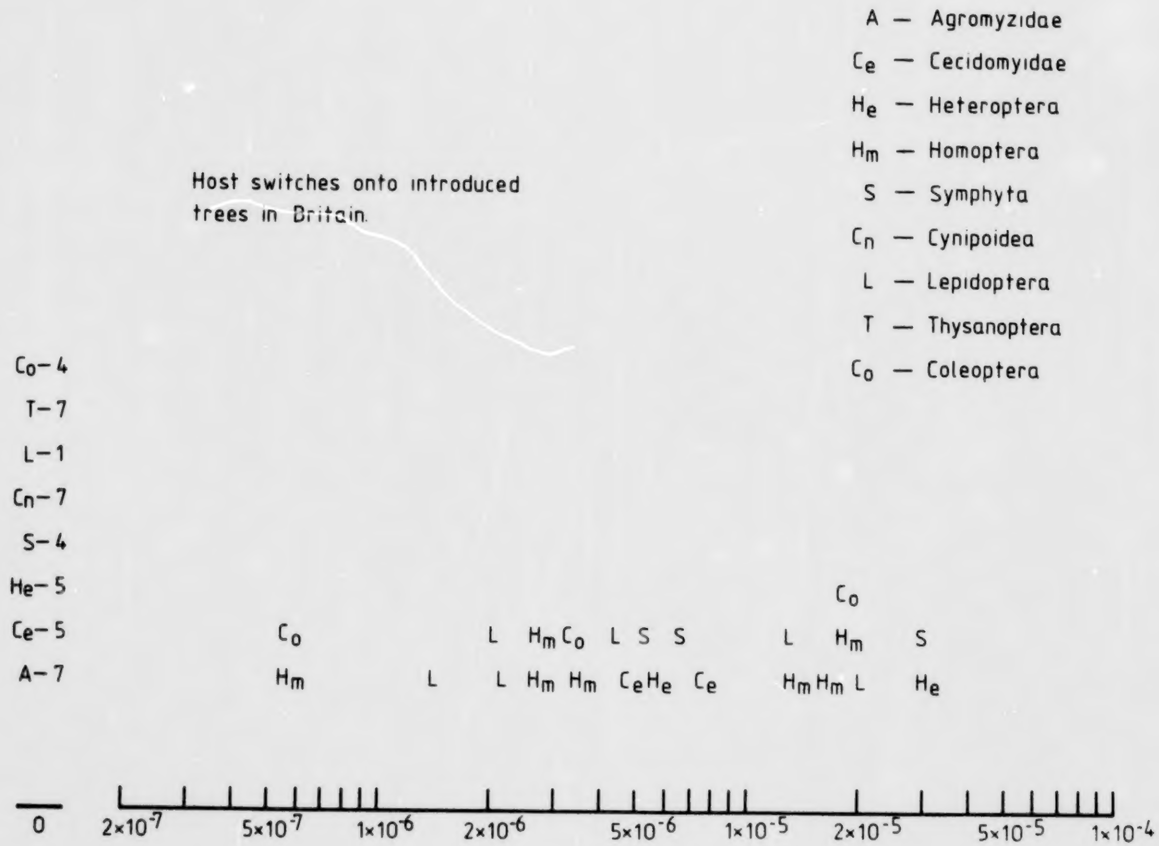

Fig. 1. Probabilities of a host-shift (insect species, plant species^{-1} year^{-1}) calculated from the data in Table 1 (see text for details).

sites, and 'apparent competition' from polyphagous enemies (Holt 1977) or what Jeffries and Lawton (1984) called competition for 'enemy-free space' (see also Price 1981). For insects feeding on plants, competition for enemy-free space seems more likely than conventional competition (Lawton and Strong 1981; Strong *et al.* 1984). The concept of competition for enemy-free space is elaborated in more detail below. Here it is sufficient to note that invasion of native plants by introduced biological control agents may be greatly impaired by the natural enemies of resident insects, just as some biological control agents have failed to establish on target plants because of the ravages of resident enemies that 'spill over' from other prey and plants (Goeden and Louda 1976). It is difficult to estimate by how much risk should be adjusted for the enhanced difficulty of switching to native plants and well-established crops. A conservative guess is that probabilities of attacking such hosts lie in the range 1×10^{-8} to 1×10^{-7} insect species, plant species^{-1} year^{-1}.

Clearly these calculations are very crude, and could be improved, although they start with excellent data (Table 1) for one of the best studied floras and faunas in the world. Difficulties and uncertainties aside, I think they are sufficient to illustrate why well over 100 insect biological control agents (Batra 1981; Julien 1982) have been exposed to 1000s of species of non-target plants for more than 75 years without anything untoward going wrong.

Starvation Trials

Whilst so low a probability of the unexpected happening is comforting, it is not the only, or even perhaps the main concern of many biological control workers. One of the most vexing problems is how to interpret results from screening trials done under highly artificial conditions, suggesting that potential control agents will eat one or more species of non-target plants, at least when they are starving. These problems have recently been cogently addressed by Andres (1981), Dunn (1978), Harris (1985), Schroeder (1983), and Zwölfer and Harris (1984), amongst others, and I do not propose to repeat their arguments here. The following points do, however, seem worth making.

Successful colonisation of a new host plant (i.e. establishment and maintenance of a population on that plant) requires far more than a willingness for starving insects to eat it. Starving people will eat cats, rats and shoe leather, but this information is not useful for predicting what I normally eat for lunch. Stenophagous insects — the type that make good biological control agents — usually have a suite of morphological adaptations and characteristic behaviours all intimately linked to their host plant(s), fulfilling specific adult mating and ovipositional requirements, as well as determining larval success and adult longevity (Bush and Diehl 1982; Diehl and Bush 1984; Futuyma 1983; Futuyma *et al.* 1984). The mechanisms determining host shifts in such insects are still not well understood, but they *do not* simply involve a willingness to feed when starving. A better understanding of these problems will undoubtedly arise from careful studies on the genetics, behaviour and general biology of host races on different species of plants, currently being carried out by several groups, for example Booij (1982), Claridge and Hollander (1983), Futuyma *et al.* (1984), Singer (1983), and Wood and Gutman (1983).

Futuyma *et al.* (1984) suggested that divergence in host utilization occurs first via genetically determined changes in behaviour, rather than by physiological adaptations to the novel host. It remains to be seen whether their results for fall cankerworm generalise to other species. But there is no doubt that although host selection behaviour in the field deserves more study, a species' behaviour in starvation tests bears little resemblance to its behaviour in the field. Intriguingly, although one of the earliest optimal foraging models (Levins and MacArthur 1969) was developed specifically for herbivorous insects, later studies have focussed almost entirely on predators or seed-feeders (see Krebs and Davies 1984). Exceptions are Lacher *et al.* (1982), Rausher (1978, 1981), and Schultz (1983). Foraging theory developed for predators does not extend easily to herbivores, but virtually all existing data and models, be they for herbivores or carnivores, point to strong evolutionary constraints on foraging behaviour. As a result, animals in the field are invariably choosey about where they feed and what they feed upon, avoiding unprofitable or risky feeding sites (Krebs and Davies 1984). Starvation trials, by putting animals at maximum risk, make it profitable for them to try to eat almost anything rather than die. Not surprisingly, they eat things when starving that they would *never* eat in the field. Sensible feeding trials must therefore incorporate sufficient realism for the animal to exercise choice, preferably both about where to eat (or oviposit) and which plant(s) to select. Dunn's (1978) proposals are admirable in this regard. By totally ignoring existing foraging theory and data, starvation trials give quite the wrong impression of risk, and impose highly artificial and unnecessary constraints on biological weed control.

Using Exotic Insects to Control Native Weeds: The Case of Bracken Fern

Biological control has been attempted much more frequently against imported weeds than it has against native weeds. Julien (1982) for example documents biological control programmes against 86 naturalised weeds compared with 25 native weeds. In part, such data merely reflect the fact that many important weeds are aliens. Nevertheless, the use of exotic insects to control native weeds has been virtually ignored, an important exception being the control of *Opuntia* (Cactaceae) on Santa Cruz Island, California, by *Dactylopius* (Homoptera: Dactylopiidae) (Goeden and Ricker 1980). I propose to devote the remainder of this paper to a native weed that is a prime candidate for biological control, namely bracken fern (*P. aquilinum*) in Britain, outlining how detailed ecological studies have pinpointed at least one, and possibly more, potential exotic control agents.

The Nature of the Problem

Dense, more or less pure stands of bracken now cover thousands of hectares of hill land in Britain, land that is used primarily for hill farming, forestry, water catchment areas and recreation. The plant is a major weed for the following reasons: (a) It has spread dramatically during the present century, and continues to do so at between 2 and 4% a year. Reasons for the spread are discussed by Page (1976). Spread of bracken leads directly to loss of grazing, makes shepherding very difficult, and provides a reservoir for sheep ticks. (b) Bracken is a very toxic plant (Jones 1983) and although normally avoided by stock, they occasionally eat sufficient to cause poisoning and death. (c) One of the toxins in bracken is a carcinogen, detectable in milk from cows grazing on hill land, and a potential hazard in human water supplies from bracken-infested catchment areas (Taylor 1980; Hoever. *et al.* 1983). (d) In some areas, e.g. the North Yorkshire Moors, bracken is a serious problem on grouse moors, where grouse shooting for sport is a valuable source of income to landowners (Dr. G.R. Potts, Game Conservancy, pers. comm.). (e) In recreation areas, bracken impedes access by the public, and adversely affects natural vegetation and the appearance of beauty spots.

Bracken control by spraying or repeated cutting (e.g. MAFF 1974; McKelvie and Scragg 1972/3) is expensive, difficult, and usually impermanent. In Scotland, *c.* 2 000 ha are treated each year (a mere 1% of infested land) at a total cost of £200 k. Despite control, bracken in Scotland is estimated to be spreading at 7 000 ha per annum. In 1982 the North Yorkshire Moors National Park (one small part of Northern England) estimated that £35 k was spent on bracken control from the Public Sector, and £40 k from the Private Sector. This control at best is effective for only 3–4 years (Dr. R. Brown, North York Moors National Park staff, pers. comm.). The Yorkshire and Scottish figures suggest that total costs of bracken control in Britain must easily exceed £500 k per annum, not including figures for lost grazing, stock poisoning, etc. Although by the standards of some weed control programmes (Harris 1985; Schroeder 1983) these are not large sums of money, it has to be remembered that most bracken-infested land in Britain goes untreated because existing control methods are too expensive or impossible to use because of the terrain. Under these circumstances, biological control may provide an ideal solution.

The Native Insect Fauna of Bracken

Detailed studies on the ecology of British bracken-feeding insects have been carried out by colleagues and myself at York since 1971. Some 27 species of native insects feed on bracken in Britain, with others doing so occasionally (Lawton 1976, 1982). None significantly damages the plant, not because the plant is toxic to them, but because they are in the main kept rare by their own natural enemies, parasitoids, predators and diseases. Experimentally released from the impact of enemies, some British native insects build up to large numbers and extensively damage the plant (Lawton 1984*a*, *b*). Imported insects similarly released from natural enemy control might reasonably be expected to cause extensive damage to bracken.

Where Might Suitable Biological Control Agents be Found?

The same species of bracken grows naturally on every continent except Antarctica. The herbivore fauna found on the plant is very different in each geographical region (Lawton 1982, 1984*b*); hence there should be no shortage of possible biological control agents feeding on bracken outside the British Isles. Of course, bracken is not identical in all parts of the globe. The taxonomy of the plant is complex (Page 1976), with two major subspecies each with several varieties. In the first instance, suitable control agents should be sought in areas with the same subspecies as Britain (*P. aquilinum*, subspecies *aquilinum*); i.e. in North America, Africa, or Asia and the Far East. This is not to say that insects associated with subspecies *caudatum* (found primarily in South America and Australasia) would not make suitable control agents for subspecies *aquilinum*, but matching subspecies may increase the changes of success (see Harris 1985 for a brief discussion of the problem of host varieties).

The Characteristics of an Ideal Control Agent

An ideal control agent for bracken in Britain must: (a) come from a temperate, seasonal climate; (b) be bracken specific and capable of imposing significant damage to the plant; (c) feed in a way that is different from any native British species; and (d) be taxonomically distinct from native British species.

Requirements *c* and *d* specify that the ideal control agent ought to occupy a currently vacant niche (Lawton 1982). This requirement is not to prevent exclusion of exotic control agents by conventional interspecific competition, which appears to be negligible amongst British bracken-feeding insects (Lawton 1982, 1984*a*, *b*), but to prevent exclusion via 'apparent competition' (Holt 1977) or competition for 'enemy free space' (Jeffries and Lawton 1984) from the natural enemies of resident British bracken-feeding insects.

The conditions for a new species, j, to invade and establish itself in a community where it is subject to attack by resident natural enemies have been formally stated by Holt (1977). They are:

$$r_j > a_j P. \tag{2}$$

where: $r_j =$ intrinsic rate of increase of the invading species j; in this case j is the species to be released as a biological control agent; $a_j =$ attack rate (or area of discovery [Hassell 1978]) of an established enemy population on species j; and $P =$ density of established polyphagous enemies, sustained by resident herbivore species, but capable of attacking the biocontrol agent, j.

Characteristics of species j that reduce a_j, for example their taxonomy or feeding site, will favour j's establishment in the community. Clearly, the more species j differs from victim populations already in the community the less likely enemies are to recognise it as food or hosts, and the more likely species j is to establish and spread.

One species is currently thought to fit all these criteria, a moth *Parthenodes angularis* Hampson (Lepidoptera: Pyralidae) from the Katburg Mountains and elsewhere in South Africa (identity confirmed by Mr. M. Shaffer, British Museum). One or more caterpillars mine the rachis (stem) and by cutting the vascular bundles greatly stunt the growth of the frond. Preliminary field work carried out by Professor V. C. Moran and myself in South Africa suggests that *Parthenodes* is bracken specific; we found it in no other ferns, nor has it ever been reported as a pest of any plants anywhere in South Africa. Yet damage to bracken was often extensive and heavy. No native British insects cause damage to bracken as does *Parthenodes*, and none of the British bracken-feeding Lepidoptera are Pyralidae. Finally, and most conveniently, bracken in the Katburg Mountains is the same subspecies and variety (subspecies *aquilinum* var. *aquilinum*) as British bracken, and the climate is very similar to that in Britain.

Two other possible control agents also live on bracken in the same area, but much less is known about them. They are again very different from native British bracken-feeding insects. They are *Eupteryx maigudoi* Dworakowska (Homoptera: Typhlocybini), apparently bracken-specific, and an unidentified eriophyid mite that causes extensive damage and distortion of the fronds. Bracken is such a persistent, vigorous plant that it will almost certainly be necessary to release more than one species of control agent against it (Harris 1981*b*, 1985).

What Next?

At the moment, permission to import *Parthenodes* into Britain under quarantine has been made in collaboration with CIBC; grant support for the work has been approved by the Agricultural and Food Research Council, and screening will commence early in 1985. We also need to find out more about the other possible control agents, and to search other likely localities. On climatic grounds, Chile looks a suitable area, although bracken there is subspecies *caudatum*. Only when *Parthenodes* has been screened, and other possible control agents located and studied will we be in a position to contemplate releases in Britain. Since biological control of weeds has never been attempted in this country, the decision whether or not to release will have to be taken after the widest possible discussions with all interested parties. Harris (1985) has some exemplary comments to make on these problems, but for the moment, they lie outside the scope of this paper.

Finally, it should not have escaped the reader's notice that *Parthenodes* could make an ideal control agent for bracken elsewhere in temperate regions where native bracken is spreading and causing serious problems; mainland Europe and New Zealand are two such areas.

General Lessons

I do not believe that bracken is the only native weed that is suitable for biological control using exotic insects. The general criteria are: (i) A weed that is native in at least two different parts of the world, or with at least close relatives in other parts of the world from which suitable control agents might be collected. (ii) A distinct insect fauna in different geographical regions, to provide a pool of potential control agents. This condition seems to be typical of most plants (Strong *et al.* 1984). (iii) Good ecological studies on the resident insect community attacking the plant in areas where it is a weed to discover (a) why resident insects are ineffective as control agents and (b) vacant niches suitable for exploitation by control agents.

Of course there is no guarantee that suitable control agents fulfilling all these criteria will exist, particularly insects that are capable of inflicting damaging control on the weed, and are safe. But there is no guarantee, either, that we can continue to develop new and better herbicides for weed control as resistance (Gressel 1984) and economic constraints pose increasing problems. I believe the time is now ripe to pay more attention to the possibilities of biological control of native weeds.

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Consequences of Species Introductions and Removals on Ecosystem Function — Implications for Applied Ecology

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Abstract

Species may be added to or removed from ecosystems without greatly affecting ecosystem function. Popular assumptions about delicate balance of ecosystem processes relative to plant species composition when examined in terms of: (1) paleoecological; (2) historical; and (3) current biochronological and biogeographical sequences are found lacking. Species composition of vegetation is shown to vary continuously in time as well as space. Natural ecosystems exhibit greater stability (inertia) in physiognomic structure and functional processes than in species composition. Characteristics of vegetation dynamics have important implications in applied ecology and the use of biological control in vegetation management.

The above generalizations are based on studies summarized as follows: (1) Creosotebush is a recent addition to the vegetation of the Chihuahuan, Sonoran and Mojave Deserts. In a short period of 11,000 yrs it has become a dominant component of the vegetation over many millions of hectares. The macrofossil record indicates a dynamic invasion from south to north with a continuing trend toward proportional increase over time. Some clones in the southern Mojave have reached great age (> 5000 yrs) and may represent members of the initial establishment population. A limited number of generations preclude the possibility of co-evolution proceeding to the point of establishing highly integrated and biologically regulated communities. (2) Similar dynamic changes are evident in paleoecological chronologies obtained from pollen stratigraphic profiles of the eastern deciduous forests of North America. The northward migration of the principle tree species (oaks, maples, hickories, etc.) has varied in rate (100-400 m/yr) and direction, and as a consequence, arrival times (as recent as 2000 yrs ago) in extant forest stands. Natural changes in modern forests indicate that shifts in species composition have continued into the present. (3) Similar kinds of dynamic changes are noted in the constant assembling and reassembling of species comprising the purportedly 'ancient forests' of the tropics. (4) Modern changes in the flora of California through introductions and extinctions have netted a substantial increase in species richness and probably diversity. Introduced species approximate 16% of the flora. Many aliens are primary contributors to ecosystem productivity and may be considered 'new natives'. Few extinctions are evident. Many indigenous species are only minor components of the ecosystem in which they are found. (5) Accidental and/or purposeful biological control episodes have seldom resulted in the complete removal of plant species from ecosystems. Worse case scenarios featuring American chestnut, American elm and eastern hemlock, show that biological control agents have the capacity of greatly altering the roles particular species play in natural ecosystems. Other species responded quickly to fill the gaps and maintain functional structures and processes. Similar responses resulted from purposeful application of biological control to both native (manuka and prickly pear) and introduced (Klamath weed and prickly pear) rangeland weeds.

Conséquences de l'Introduction et du Retrait d'Espèces sur l'Écosystème — Répercussions sur l'Écologie Appliquée

Certaines espèces peuvent être ajoutées à des écosystèmes ou en être retirées sans modifier sensiblement la fonction de l'écosystème. Les hypothèses populaires au sujet de l'équilibre délicat des mécanismes de l'écosystème appliqués à la composition des espèces végétales examinées en termes de successions paléoécologiques, historiques, ainsi que biochronologiques et biogéographiques, s'avèrent plutôt rares. En effet, la composition spécifique de la végétation varie continuellement dans le temps et dans l'espace. Les écosystèmes naturels affichent une plus grande stabilité (inertie) dans leurs structures physiognomiques et leurs mécanismes fonctionnels que dans leur composition spécifique. Les caractéristiques de la dynamique de la végétation ont des répercussions importantes en écologie appliquée et sur l'utilisation de la lutte biologique dans le'aménagement de la flore.

Les généralisations précédentes s'appuient sur des études qui se résument comme suit: (1) le creosotebush (*Larrea tridentata*) est une récente addition à la végétation des déserts du Chihuahua, Sonora et Mojave. En l'espace d'une brève période de 11 000 ans, le creosotebush est devenu une composante dominante de la végétation et occupe maintenant plusieurs millions d'hectares. Le répertoire des macrofossiles révèle une invasion dynamique du sud vers le nord avec une tendance continue vers un accroissement proportionnel dans le temps. Certains clones dans le sud du Mojave ont atteint un âge avancé (plus de 5 000 ans) et pourraient être des représentants du premier peuplement établi. Un nombre limité de générations écarte la possibilité d'une co-évolution vers l'établissement de communautés végétales hautement intégrées et biologiquement contrôlées. (2) On peut observer une évolution dynamique analogue dans les chronologies paléo-écologiques tirées de profils stratigraphiques de pollens des forêts cadugues de l'est de l'Amérique du Nord. La migration vers le nord des principales espèces arborescentes (chênes, érables, caryers, etc.) a varié en vitesse (100 à 400 m/année) et en direction, et par conséquent, dans l'époque d'arrivée (aussi récente qu'il y a 2 000 ans) dans les peuplements forestiers existants. Les variations naturelles rencontrées dans les forêts modernes révèlent que certaines transitions dans la composition spécifique se poursuivent encore aujourd'hui. (3) Le même genre d'évolution dynamique apparaît dans le groupement et le regroupement constant des espèces qui composent les soi-disante 'anciennes forêts' tropicales. (4) L'évolution moderns de la flore de la Californie par des introductions et des extinctions a entraîné un accroissement net substantiel de la richesse des espèces, et probablement de leur diversité. Les espèces introduites composent environ 16% de la flore et de nombreuses introductions contribuent essentiellement à la productivité de l'écosystème et peuvent donc être considérées pour cette raison comme 'nouvelles espèces indigénes'. On n'observe que de rares cas d'extinction. Beaucoup d'espèces indigènes ne forment que des composantes secondaires de l'écosystème dans lequel on les retrouve. (5) Aucun épisode de lutte biologique, qu'il soit accidentel ou intentionnel, n'a pu entraîner le retrait définitif d'espèces végétales des écosystèmes. Le châtaignier d'Amérique, l'orme d'Amérique et la pruche du Canada sont de tristes exemples qui rélèvent que les agents de lutte biologique sont capables de modifier considérablement le rôle que certaines espèces jouent dans les écosystèmes naturels. D'autres espèces réagissent alors rapidement pour combler les trous et maintenir des structures et des mécanismes fonctionnels. En effet, l'application préméditée de la lutte biologique à des mauvaise herbes indigènes (leptosperme et figuier de Barbarie) et introduites (millepertuis commun et figuier de Barbarie) de parcours a produit des réactions analogues.

Introduction

The relationship of the title of this paper to the biological control of weeds may not be immediately self-evident. At the outset then perhaps it is worthwhile to assert its presumed relationship to a major theme of the VI International Symposium on Biological Control of Weeds, i.e. 'conflicts of interest'. A tie with conflict bears directly on questions such as the propriety of *introducing* exotic insects to *remove* or reduce the abundance of native plants that are behaving as weeds on rangelands.

Questions of propriety in this regard usually revolve around assertions about the effects that such actions will have on other parts of the biological system and in particular on the ecosystem as a whole. Changes in ecosystems can be framed in terms of shifts in structure and function as reflected by stability, diversity, and productivity measures. Our attention will be directed toward stability, which has several conceptual components and in theory is often linked closely with diversity and productivity. Ecosystem stability has at least two principle aspects: (1) that related to the toughness of the system, i.e. how much force is required to change its structure and/or function; and (2) that related to its response after an alteration has occurred. Westman (1978) discusses the first aspect in terms of inertia and its measurements and the second under the heading resilience, which he separates into the purportedly measureable components of elasticity, amplitude, hysteresis and malleability. The usual perception of inertial stability is in terms of species structure, i.e. the number, size, age, etc., of individual species, which in the proverbial 'balance of nature', constitute a self-sustaining system. An alternative view of a self-sustaining system may also be held in terms of physiognomic structure and functional processes in which various species with similar physiognomy and function are interchangeable. In the latter case a system may have high inertial stability even with the coming and going of species. The idea is that a steady state condition in terms of processes can be maintained in the absence of species population equilibria. As for the resilience of altered ecosystems, consideration of elasticity (the capacity for recovery) and malleability (the capacity for establishing a new structural or functional balance) are perhaps the two most significant parts of the concept for our discussion.

The ecosystems envisioned for purposes of this presentation are those that constitute native rangelands. Westman (1977) speaks of the structural components of such ecosystems as comprising nature's free 'goods' (e.g. forage, timber, fish, etc., that are marketable products), and the functional processes which drive them as providing nature's free 'services' (i.e. fixation of atmospheric nitrogen, energy capture through photosynthesis, breakdown of pollutants, maintenance of oxygen levels in the air, binding of the soil, etc.), which in short are those things that insure 'clean air, pure water and a green earth'. Westman asks the question, 'How much are nature's services worth' and Pimental *et al.* (1980) try their hand at calculating some of the values for the United States in economic terms and conclude that they are enormous.

Now, in terms of the biological control of weeds, which is one aspect of applied plant ecology, there is a common sentiment abroad, particularly in the United States, that organisms that are exotic (in this case insects) should not be used to control organisms that are native (in this case weeds). This sentiment seems to depend in large part on the assumptions that: (1) native species are essential pieces of delicately balanced co-evolved ecosystems that are stable through time and replicated in space (Andres 1981*a*, *b*; Pemberton 1985); and (2) native species and introduced species are fundamentally different in the roles they play in ecosystems (Howarth 1983). Indeed Andres (1981*b*) maintains that 'Ecological conflicting interests arise in the belief that all elements of an ecosystem are interrelated and that removal of a plant species from an area, especially a native species, will trigger some unknown and unwanted reactions.' and Howarth (1983) speaks of 'biological pollution' defined as 'the establishment in the wild of foreign or non-native organisms' and challenges the biological control method in terms of its 'environmental compatibility' which is often used as a principle argument in favor of the method (Harris 1977). Both Andres and Howarth ascribe much higher 'environmental value' to organisms with native status than to those that are alien.

The views just presented are most easily understood in terms of ecological theory formalized by Frederic Clements and his followers in the first half of this century. Clements perceived vegetation units as being highly integrated and regulated entities serving as the matrix for biotic assemblages representing discrete steps of biological organization, i.e. super organisms. As such, vegetation units arose, grew, and matured through processes of ecological succession and reproduced themselves by perpetuating the more or less final stable climax state. Stability in structure came to be viewed primarily in terms of species, i.e. each species in its proper proportion was important in making the climax what it was. Climax vegetation was considered ancient in age. Climatic change resulted in death of the climax organism or its shift to a new location trailing the climate (Clements 1916, 1920; Weaver and Clements 1938; Dyksterhuis 1946, 1949).

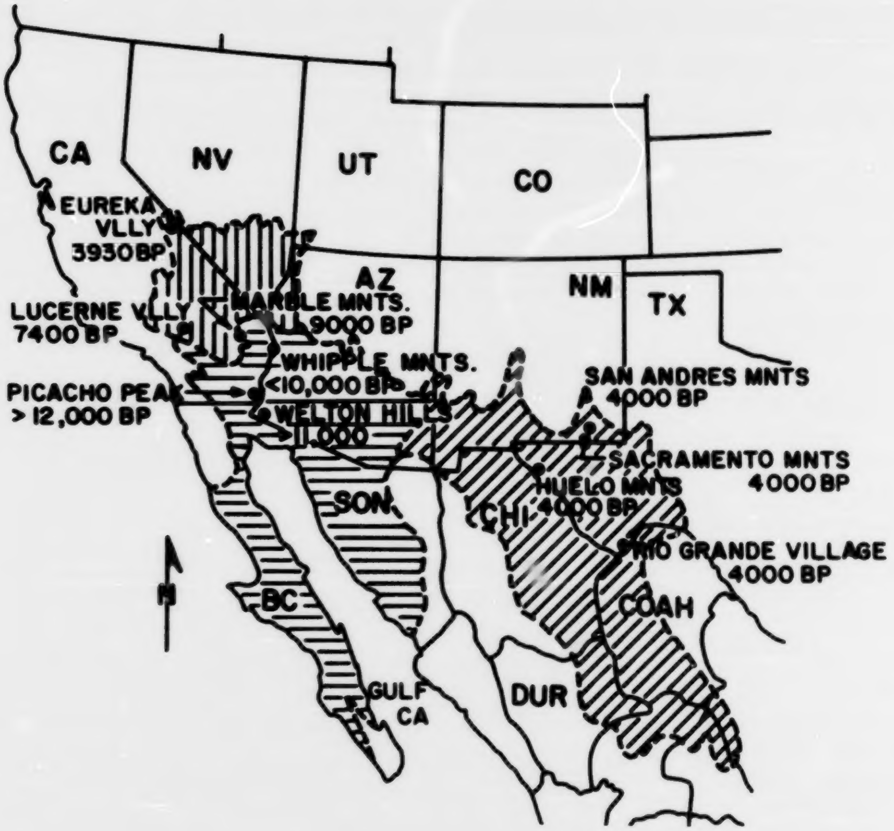
The formalized climax concept has had enormous appeal through the years particularly to animal ecologists and those working in applied fields of biology (e.g.

animal populations ecology and range management) where there is a need to relate vegetation dynamics to other considerations (Allee *et al.* 1949; Price 1975; National Range Handbook 1976; Meeker and Merkel 1984). Clementsian climax theory has not been nearly so readily accepted in its home discipline of plant ecology, although it is without doubt one of the most discussed subjects in plant ecological literature. The antithesis of the Clementsian climax theory is Gleason's individualistic hypothesis on the origin of plant communities (Gleason 1926). I have no intention of rehashing the differences in the two points of view here since it has been done many times by others. I would observe, however, that from my perspective, current theoretical research on the nature of vegetation, a very active field, leans much more strongly in the direction pointed by Gleason than that by Clements (Miles 1979; McIntosh 1980; Vale 1982). Theoretical questions on this matter should not be dismissed lightly as having significance only in academia. It must be realized that the generally accepted vegetation dynamic theory plays a crucial role in setting the mood for enactment of public policy and law in essentially all matters concerning our environment.

My perspective is presented from the position of a plant ecologist and not as a technical expert in biological weed control as are most of the contributors to this Symposium, including my colleagues from the USDA, ARS Laboratory in Temple, Texas. The latter have more than a casual interest in the stated subject matter since their primary research mission is to develop biocontrol technology for the management of southwestern North American rangeland weeds, most of which are native species and structural components of natural ecosystems. The critical assertions concerning balanced, co-evolved systems and biological pollution cited above seem to presuppose certain things about species, communities, and ecosystems that need to be examined more closely in terms of current knowledge and theory, particularly in regard to the origin and distribution of species, community structure and vegetation development, and ecosystem equilibria. I do not presume to have the expertise needed to give complete coverage to these matters here but will present some personal observation, examples from the literature and thoughts in these regards that may bear on the assessment of risks involved in attempts to manipulate native rangeland weeds using biological control agents.

The Case of Creosotebush

First I will consider some aspects of the natural history of creosotebush, *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. (Zygophyllaceae), in particular how it came to occupy its present position in the warm deserts of North America. Furthermore, it has been identified as a possible candidate for biological control (DeLoach 1981). Today *L. tridentata* is *the* plant, i.e. the principle component of the vegetation, of the Chihuahuan, Sonoran and Mojave deserts (Fig. 1). It is certainly a nominee for the world record for the shrub species dominating the largest geographical area on earth. On each desert it is represented by a different chromosome race, i.e. diploid on the Chihuahuan, tetraploid on the Sonoran and hexaploid on the Mojave (Yang 1970); the races are not readily distinguished except on the basis of chromosome number. *L. tridentata* has close taxonomic affinities with *L. divaricata* Cav. of the Argentine desert in South America and has in fact been considered conspecific with it by some investigators (Hunziker *et al.* 1972). *L. divaricata* in South America is diploid, matching the race of *L. tridentata* of the Chihuahuan desert. The generally accepted interpretation of events connecting them and leading to the present distribution pattern is that the *L. divaricata* type from South America (more than one species of *Larrea* occurs there) was introduced through processes of long distance dispersal to the Chihuahuan Desert in North America. From there it spread northwestward to the Sonoran and Mojave desert undergoing cytogeographic differentiation in the process (Wells and Hunziker 1976). The thing most significant about this spread for our consideration is the time frame in which it occurred.


CA
NV
UT
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AZ
NM
TX
EUREKA VLLY 3930 BP
LUCERNE VLLY 7400 BP
MARBLE MNTS. 9000 BP
WHIPPLE MNTS. <10,000 BP
PICACHO PEAK > 12,000 BP
WELTON HILLS 11,000
SAN ANDRES MNTS 4000 BP
SACRAMENTO MNTS 4000 BP
HUELO MNTS 4000 BP
RIO GRANDE VILLAGE 4000 BP
SON
CHI
COAH
BC
GULF CA
DUR
N

Fig. 1. The Deserts of southwestern United States and Mexico: ▥ = Mojave Desert; ▤ = Sonoran Desert; ▨ = Sonoran Desert; Named locations are places with appropriate series of ^{14}C dated packrat middens. The numerals indicate the approximate date that *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. arrived at that point. AZ = Arizona, BC = Baja Calif., CA = California, Chi = Chihuahua, Coah = Coahuila, NM = New Mexico, NV = Nevada, TX = Texas, Son = Sonora, Dur = Durango.

A method of dating the expansion phase has been fortuitously provided through the peculiar activities of some attractive small rodents belonging to the genus *Neotoma*, known variously as packrats or woodrats, and the innovative perception of Dr. Philip Wells, who recognized a unique opportunity for paleoecological investigations (Wells and Jorgensen 1964). Packrats, long time residents of the deserts, have an apparent fetish for collecting and stockpiling in their nests samples of all manageable objects that occur within their home ranges, including the plant life. Nests or middens constructed from these materials can attain sizeable proportions when inhabited by successive generations of rodents and when located in sheltered places can persist almost indefinitely. Dr. Wells recognized that the resulting deposits provided a chronological record of the plant life that had occupied the home range areas through the rats' generations of time. Carbon-14 dates of *Neotoma* nests span the period from present to over 40,000 yrs ago (Wells and Berger 1967). Many middens from all three deserts have now been located and analyzed. The focus of the research effort has generally been directed at utilizing fossil middens for timing the disappearance and elevational shifts in conifer woodlands as a surrogate measure of climatic change (Wells and Berger 1967; Wells 1976; Van Devender and Spaulding 1979). In keeping with this emphasis, middens containing fragments of juniper, pine and other conifers were particularly sought out for plant composition analysis and ^{14}C dating, especially in those areas now occupied by desert shrubs, the most abundant of which is, as stated earlier, creosotebush.

Today modern midden deposits in creosotebush-dominated areas contain an abundance of *Larrea* fragments (Wells 1974, 1976; Cole and Webb, *in press*). Yet in the fossil middens older than 11,000 yrs, there is essentially a dearth of creosotebush even though some other modern desert species' macrofossils (e.g. agaves, yuccas, and opuntias) do occur (Wells 1983; Van Devender 1984). This pronounced pattern was central to Wells and Hunziker (1976) suggesting the intriguing possibility of a relatively late introduction of *Larrea* from South America. The actual date of introduction is difficult to establish but the rate and direction of spread after its confirmed presence in North America can be determined.

The oldest macrofossils of *Larrea* reported so far are from low rainfall, low elevational portions of the Sonoran desert not far distant from the path followed by the Colorado River as it follows its course through the desert to the Gulf of California (Fig. 1). *Larrea* begins to appear consistently and in quantity in middens of this region about 11,000 years ago (Table 1); younger ages are associated with deposits toward the northwest, e.g. Marble Mountains ≈ 9000 yrs, before present (B.P.), Lucern Valley ≈ 7400 yrs B.P., Eureka Valley ≈ 4000 yrs B.P. An invasion time series from the mouth of the Colorado River in the Sonoran Desert to the northern limit of the present *Larrea* distribution in the Mojave Desert is thus evident (Fig. 1). In the Chihuahuan Desert creosotebush arrived at its northern limit at about the same time as in the Mojave, i.e. approximately 4000 years ago (Table 1). I have found no reports of macrofossils of *Larrea* from the central or southern Chihuahuan Desert areas, even though cytogeographic patterns strongly suggest that this is the area where the oldest ancestral fossils should be sought.

Although the 'thousands of years' time frame of this discussion may at first seem irrelevant to the usual time scale of concerns of our modern society (i.e. years, decades, and centuries), I submit that in view of the enormous expanses and long linear distances involved it does have immediate relevance. The present north–south range of creosotebush from approximately 23° to 37° latitude spans a diagonal distance of about 2000 km. The area of the three deserts invaded is estimated at around 100 million ha. Using a time frame of 7000 yrs (i.e. 11,000–4000 B.P.) the rate of movement required to attain the distribution evident in the macrofossil record, assuming a south to north expansion, would be on the order of 280 m/yr or 2.8 km/decade. The occupancy of newland area would need to proceed at a rate of about 16,000 ha/yr. Such dynamic change casts serious doubt on popular suppositions about long-term balance and delicate equilibria in the natural landscape before the advent of modern man.

Another significant point in the saga of creosotebush concerns its longevity. Plants in the Mojave desert have been found to develop clonally and live to great age (Vasek *et al.* 1975; Sternberg 1976). Clones are readily distinguished on aerial photographs by irregular donut-shaped growth patterns (Fig. 2). Ages are extrapolated on the basis of clone size and measured rates of clone growth. Growth rates have been estimated using a variety of techniques, including time-lapse photographs, radio carbon dates of dead clonal segments and radial growth-ring increment determinations (Johnson and Vasek 1975; Vasek 1980). Clone diameter growth rates vary with substrates but are generally on the order of 2 mm/yr. Clones up to 21 m across are known. Extrapolated ages for the older individuals in the vicinity of Lucern Valley, California (Mojave Desert), range from 6000 to 11,000 yrs depending on the growth rate increment used (Sternberg 1976;

Table 1. Dates of plant macrofossil assemblages preserved in packrat middens from localities in the Mojave, Sonoran and Chihuahuan Deserts currently dominated by creosotebush, *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. (LATR). Data selected from localities where concentrated sampling provides extended chronological sequences of ^{14}C dates that permit reasonable bracketting of the time period of LATR arrival.

	Years Before Present LATR Time Bracket			
Location	Absence	Presence	Comments	Source[1]
Mojave				
Eureka Valley, CA	6795	3930	LATR in low abundance after first appearance but increases markedy in time.	(1)
Mojave Northern	5595	2635		
Limit	5435 (?)[2]	1580		
Ord Mnt., CA	9140	7400	Sites located in close proximity.	(2)
Lucerne Valley, CA (South-Central Mojave)	7800	5880		(3)
Marble Mnts., CA	10465	8925 (?)	LATR low abundance at first appearance.	(1)
Transition from	10210	7930		
Mojave to Sonoran	9515 (?)	5520	Increases to position of dominance.	
	8905	4475		
Sonoran				
Whipple Mnts., CA Northern Sonoran	9980	(—)[3]	Presence of LATR not reported.	(4)
New Water Mnts., AZ Northern Sonoran	7870	10800	Some sites evidently continued longer without LATR than others.	4, 5
Welton Hills, AZ Southwestern, AZ	(—)	10580		2
Picacho Peak, CA Southeastern, CA	(—)	12730	Most arid part of Sonoran Desert. Has oldest fossils.	6
Chihuahuan				
San Andres Mnts., NM (near Northern Limit)	6330	4340	Presence dates for LATR from this desert indicates a recent occupation.	7
Sacramento Mnts., NM (Southcentral, NM)	4200	3300		8
Hueco Mnts., TX (Northwest, TX)	6360	3650	North to South Age difference not evident.	9
Rio Grande Village (Southwest, TX)	5500	4300		9

[1] Sources: (1) Spaulding (1980); (2) Wells and Berger (1967); (3) King (1976); (4) Van Devender (1977); (5) Van Devender and Spaulding (1979); (6) Cole and Van Devender (unpubl. data); (7) Van Devender *et al.* (1984); (8) Van Devender and Toolin (1983); (9) Van Devender (*in press*).

[2] (?) indicates places where LATR was reported as trace but may be a contaminant.

[3] (—) indicates no data available.

Vasek 1980). Radio carbon dates of packrat middens from the same vicinity show *Larrea* present at 5800 yr B.P. (King 1976) and 7400 yr B.P. but absent earlier than 7800 yr B.P. (Table 1). This strongly suggests that the older individual plants may represent the initial establishment of creosotebush in this part of the Mojave Desert (Johnson 1976), i.e. there is a strong possibility that members of the first generation are still present. This would seem to have a bearing on the extent to which the process of co-evolution might be regarded as a factor for establishing an integrated community functional equilibrium.

The concept of co-evolution relies on the idea that compensating adjustments occur in successive generations between, or among, interacting species to allow them to coexist. In this case there has been limited opportunity for such integration to take place due to a limited number of creosotebush generations. Indeed an argument for the recency of *Larrea* in North America is suggested by observations of relatively fewer obligatory dependent organisms and less plant consumption by insects than in Argentina where *Larrea* is purported to have originated (DeLoach, pers. comm.). I would suggest that the success of *Larrea* is due more to preadaptation than to co-evolution and that preadaptive characteristics are more often attuned to the physical environment than to biotic associates.

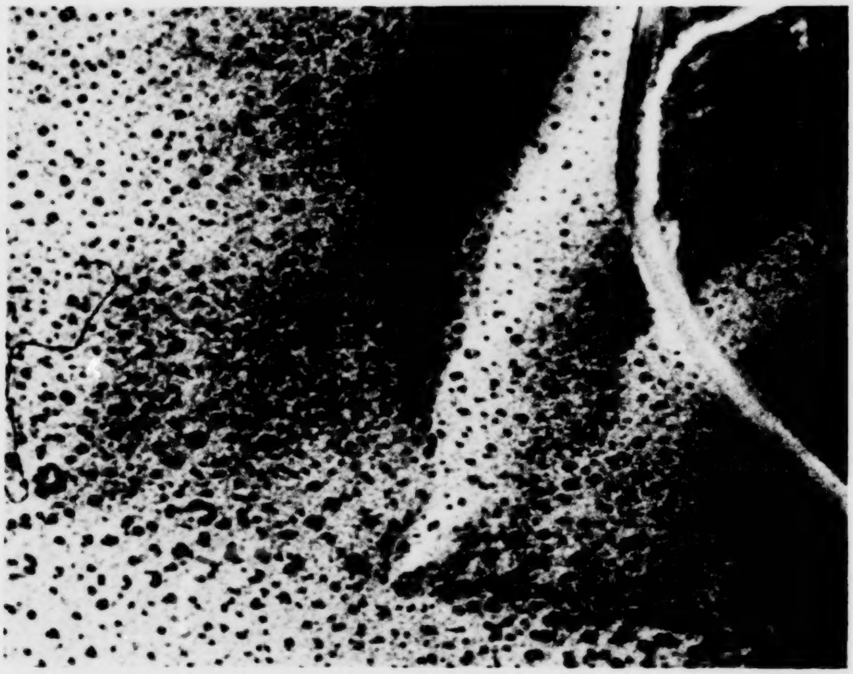

Fig. 2. Verticle aerial view of a stand of creosotebush, *Larrea tridentata* (Ses. & Moc. ex DC.) Cov., (dark globular objects) in the Mojave Desert. All stages in the development of hollow-centered vegetative clones are present, i.e. single-stemmed plants to multiple-stemmed clumps with dead centers. The large, doughnut-shaped clone on the lower left side is about 10 m in diam. and is estimated to be on the order of 5000 yrs old.

Other evidence for continuing change in desert vegetation up through modern times is also available. Cole and Webb (*in press*) sampled eight fossil and five modern packrat middens in the central Mojave in an elevational belt that included the upper limit of creosotebush and the lower limit of blackbrush (*Coleogyne ramosissima* J. Torr.; Rosaceae). Creosotebush was present in all samples, the oldest dating back 2235 yrs. Blackbrush on the other hand was not present in middens older than 270 yrs, even in areas where today it is clearly the most dominant species. This provides conclusive evidence that shifts in species composition were occurring up through the period just prior to European settlement. In the Chihuahuan Desert, the invasion of creosotebush has continued into historical times. Buffington and Herbel (1965) have documented an extensive increase in the area occupied by woody species of brush, primarily creosotebush and mesquite, on the Jornada Experimental Range in New Mexico over the past century, as have York and Dick-Peddie (1969) for scattered localities all across the southern part of New Mexico. The increase in the area occupied by creosotebush to a large extent has involved the encroachment on desert grassland, or other shrub-dominated vegetation. Some original mesquite stands, have been replaced by *Larrea* (York and Dick-Peddie 1969).

The usual explanation for the increasing abundance of brush is that grazing of the desert grassland by introduced livestock upset a 'balance' which in turn triggered brush invasion. An alternative view is that a balance never existed in the first place and that the introduction of domestic livestock just added another environmental factor that tended to modify the rate rather than the direction of changes that were already in progress. Smeins (1983) emphasizes the importance of a long-term historical perspective, for understanding the current 'brush problem'. The region of documented brush invasion in New Mexico is near the northern limit of creosotebush's distributional range and may be interpreted as the leading front of the wave of *Larrea* invasion in the Chihuahuan Desert that has been proceeding since the mid-Holocene, or about 5000 yrs (Fig. 1, Table 1).

The documented dynamics for creosotebush in the ecosystems of the three deserts indicate low inertial stability both in terms of dominant species composition and functional processes. The former is implied by the rapid invasion of creosotebush and the latter is implied by shifts in physiognomic structure, from woodland to scrub in the Mojave and Sonoran Deserts and from grassland to scrub in the Chihuahuan Desert. In terms of resilience, these systems would rank low in elasticity but high in malleability, although the observed malleableness may reflect the lack of initial and subsequent biological integration more than the disturbance of an old equilibrium and the establishment of a new one.

The question might be asked as to how representative the dynamic history of creosotebush may be of plant species in other ecosystems. After all, *Larrea* is relatively new in North America, maybe not even 'native' according to some standards. Furthermore it occupies desert habitats notorious for extremes of both moisture and temperature and the irregularity with which they are imposed. Do other species of more equable ecosystems exhibit similar dynamics?

Forest Stability

Forests are generally thought to represent the highest form of integrated vegetation development on earth. A brief assessment of the past and present dynamics of selected forest species and forest types will be presented to provide a perspective for comparison with what has been shown for *Larrea* and deserts. The principal paleoecological tool for forests is palynology, the study of pollen. Chronologically stratified sediments from forested areas, such as lake bottoms, contain pollen that permit the restructuring of the regional vegetation for periods when the sedimentation occurred. In contrast to the record preserved in packrat middens, which contain intensive samplings of all local flora, the pollen record is regional in scope and weighted heavily toward species producing relatively large amounts of wind-borne pollen.

Deciduous Forest of Eastern North America

A remarkable picture of the dynamics of tree species of the eastern deciduous forest since the last glaciation is now emerging. Three recent publications synthesize much of the available data (Davis 1981*a*, 1983*a, b*). Davis presents maps with isopleths circumscribing study sites with similar dates for the first appearance of pollen for each of the major tree genera or species in the eastern third of the United States. The invasion of trees, generally from south to north, after the glaciers melted is thus depicted (Fig. 3).

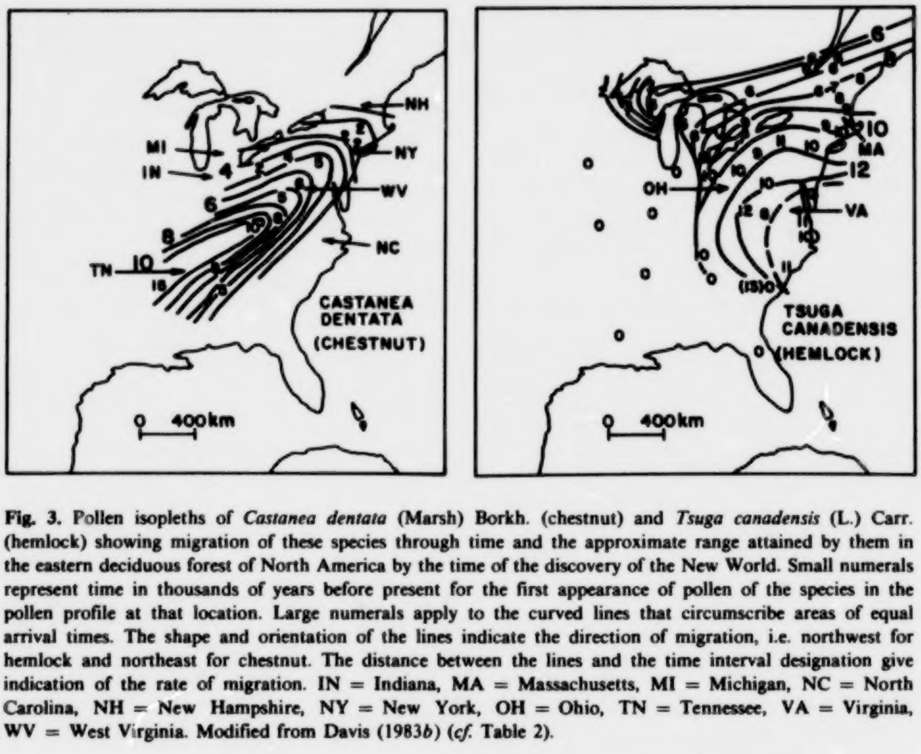

Fig. 3. Pollen isopleths of *Castanea dentata* (Marsh) Borkh. (chestnut) and *Tsuga canadensis* (L.) Carr. (hemlock) showing migration of these species through time and the approximate range attained by them in the eastern deciduous forest of North America by the time of the discovery of the New World. Small numerals represent time in thousands of years before present for the first appearance of pollen of the species in the pollen profile at that location. Large numerals apply to the curved lines that circumscribe areas of equal arrival times. The shape and orientation of the lines indicate the direction of migration, i.e. northwest for hemlock and northeast for chestnut. The distance between the lines and the time interval designation give indication of the rate of migration. IN = Indiana, MA = Massachusetts, MI = Michigan, NC = North Carolina, NH = New Hampshire, NY = New York, OH = Ohio, TN = Tennessee, VA = Virginia, WV = West Virginia. Modified from Davis (1983*b*) (*cf.* Table 2).

When maps of all contributing tree are considered, three points are strikingly evident: (1) direction of migration was different for each species/genus; (2) time of arrival at a given point was markedly different among species and/or genera; and (3) rates of movement were surprisingly fast (Fig. 3, Table 2). Documented changes in distribution and abundance spanned the entire time period between melting of the last continental glacier and the present. Rates of movement based on time increments between isopleths calculated by Dr. Davis range from 400 m/yr for jack/red pine to 100 m/yr for chestnut (Table 2). These rates are similar to those estimated for creosotebush in the desert.

The following conclusions drawn by Davis (1983*a*) are pertinent to our initial questions about balance and stability:

‘... various species of trees moved northward invdividualistically. Forest communities have represented fortuitous combinations of species during the Holocene. Many modern communities are very young; they include dominate species that have grown locally for only a few thousand years ... Evolutionary processes that may have adapted cooccurring species to one another have had very little time in which to take effect.’

The scope of short-term dynamic change in forests at the local scale is well illustrated in a novel study by Henry and Swan (1974). They considered the vegetational history of ‘... one of the rare old growth stands still undisturbed by man in central New England’. This site located in southwestern New Hampshire covers 8.1 ha of which 0.04 ha were investigated in detail. The forest history since the mid-1600s was reconstructed from the meticulous analysis of data on age and relative positions of tree parts by species in terms of standing trees, dead trees (down but unburied) and buried tree fragments. They found that three different forests had occupied the site over the last 300 yrs. A fire completely destroyed a forest made up principally of white pine (*Pinus strobus* L.; Pinaceae), white oak (*Quercus alba* L.; Fagaceae) and hemlock (*Tsuga canadensis* [L.] Carr.; Pinaceae) in approximately 1665 A.D. The forest that followed was dominated by white pine and hemlock until it was destroyed by a series of four wind storms commencing in 1897 and culminating in a hurricane in 1938. The young forest that developed following the hurricane is dominated by hemlock, beech (*Fagus grandifolia* J.F. Ehrh.; Fagaceae), red maple (*Acer rubrum* L.; Aceraceae) and black birch (*Betula lenta* L.; Betulaceae). Although the three forests have some elements in common, the differences among them suggest that the out-of-balance dynamics recorded in the palynological record persisted in the forests of eastern North America into the historical period on a local scale.

Table 2. Time span of first occurrences (years before present) of the main tree species/genera of the forests of eastern North America along a south to north gradient (*cf.* Fig. 3) and the rate of speed in m/yr (compiled from Davis 1981*a*, 1983*a*).

Species	Time span of first occurrences South North	Rate m/yr
Boreal elements		
Picea spp.	25000 to 7000	250
Larix laricina (Duroi) K. Koch	23000 to 7000	250
Pinus banksiana Lamb. and *P. resinosa* A.T.	23000 to 7000	400
Abies balsamea (L.) Mill.	21000 to 7000	200
Deciduous forest elements		
Pinus strobus L.	14000 to 2000	300–350
Quercus spp.	12000 to 7000	350
Ulmus spp.	17000 to 6000	250
Tsugu canadensis (L.) Carr.	13000 to 2000	200–250
Carya spp.	15000 to 4000	200–250
Acer spp.	14000 to 6000	200
Fagus grandifolia Ehrh.	15000 to 4000	200
Castanea dentata (Marsh.) Borkh.	15000 to 2000	100

A question on the validity of extrapolating the imbalance of forests of eastern United States to other vegetation types in the world may arise on the basis of their initial proximity to the Wisconsin ice sheet and the opportunity for invasion afforded tree species by the exposure of bare surfaces as the ice melted. A measure of the dynamics of tropical forests would provide a test for such an objection since no such available void recently freed from ice is hypothesized for the lower latitudes.

Tropical Forests

Tropical forests are notorious in their reputation for complex physiognomy and floristic diversity, which to many are synonymous with antiquity and balance. The seemingly ancient qualities of these magnificent forests were, in the days of my student indoctrination in the theory of Clementsian ecology and the dogma of climax communities, often regarded as representing a sort of end point in an ultimate plant succession; i.e. a world climax. Studies testing such notions in the tropics are not abundant, but current investigations are providing some surprising results.

A recent interpretive report of the current understanding of the dynamics of tropical forests was presented by Lewin (1984). Lewin's discussion indicates that the pollen record from tropical Central America shows much the same lack of forest species stability as was shown above for the temperate forests to the north. The work of Graham in the lowlands of Mexico is cited as concluding that tropical forests should be regarded as '... dynamic and ephemeral rather than stable and ancient'. Work reviewed from the lowlands of Guatemala, a region known as the Peten, suggests that the '... lush, moisture-loving, semievergreen, seasonal forest that now carpets the lowland' was not evident 11,000 yrs ago. Instead, the area was occupied by a juniper scrub. Lewin (1984) notes that the rate of change needed to transform the juniper scrub into the 'age-old looking modern forest' is impressive by itself but even more so in light of the probability that large portions of the presently forested areas must have regrown after having been cleared by the Mayan peoples between 3000 and 400 yrs ago.

The search for ice age refugia (i.e. places where present-day tropical forests spent the Pleistocene glaciations) have been in vain. The absence of contemporary plant species assemblages in the fossil record at particular sites requires a dynamic movement of species from different places to those sites today. Lewin (1984) sees this as casting doubt on popular concepts of community identity. 'This repeated reassembly as opposed to repeated regrowth of pristine communities, forces one to view the tropical forest as less of a cohesive natural unit than previous theory implied.'

The intuitively appealing equation that diversity results in stability has little if any support in current literature (Connel 1978; McIntosh 1980). In fact, Lewin (1984) maintains that 'high diversity through instability not stability is how the equation [now] reads'. In matters pertaining to our questions about balance and biotic integration, the tropical forests appear similar to temperate forests in lacking abstract identities that are faithfully replicated in either time or space.

Plant Species Introductions and Extinctions in California

Another perspective on the dynamics of plant diversity and the stability of species composition in the landscape may be gained from analyses of local and/or regional floras and the changes in them that occur over time. The State of California is a prime candidate for such consideration since it is relatively well known floristically and has a continuing eager cadre of amateur and professional botanists conscientiously making field observations. Even though the State political boundaries are not coincident with boundaries of recognized naturally occurring floristic units, one such unit, the California Floristic Province, falls mostly within the State (Gleason and Cronquist 1964). This gives a measure of coherence to 'political California' as a somewhat natural biotic unit to serve as framework for the floristic considerations that follow.

The earliest indications of foreign species becoming established in the State comes from the identification of plant fragments found as part of the binding material used in making adobe brick for the construction of the first Spanish mission in San Diego in 1769. Filaree (*Erodium cicutarium* [L.] L'Her. ex W. Ait.; Geraniaceae), curley dock (*Rumex crispus* L.; Polygonaceae), and sow thistle (*Sonchus asper* [L.] J. Hill; Compositae) are three introduced species so identified (Hendry 1931). These remarkable early records which date from the first European settlement, foreshadow a series of continuing waves of introductions and naturalizations of exotic plant species. As early as 1864 Bolander listed 109 species of grasses from the Central Valley of which 29 were foreign (cited by Burchann 1957). In more recent time the trend can be followed in more comprehensive floristic treatments (Table 2).

Two excellent State floras have been published: (1) 'A Manual of Flowering Plants of California' by Jepson (1925); and (2) 'A California Flora' by Munz and Keck (1959) with a supplement by Munz (1968). Three different increments of time are thus represented. Statistical summaries of these works show that 7% of the species were considered as introduced in 1925, 14% in 1959 and 16% in 1968 (Herrott and Noldeke 1956; Smith and Noldeke 1960; Howell 1972). Although differences among the tallies for the different time periods indicate changing taxonomic interpretations as well as advancing knowledge of both the native and introduced floristic components, it is most significant that the proportional increase for introduced species continues in an upward trend with time (Table 3).

Table 3. Numerical summary of reported plant species introductions to the vascular flora of California through time.

Year	No. introduced species	% of all species	Source
1925	298	7	Herriott and Noldeke (1956) from Jepson (1925)
1940	526	(?)	Robbins (1940)
1959	800	14	Smith and Noldeke (1960) from Munz and Keck (1959)
1968	975	16	Howell (1972) from Munz (1968)
1981	1022	17	Incorporation CNPS list of escapees (1981) with Howell (1972)

The very rapid encroachment of new species at the beginning of the historical period indicates the absence of initial stability in the system and perhaps what in Clementsian terms would be called a 'postclimax' situation; i.e. a condition where changes in vegetation have lagged markedly behind changes in climate. The idea is that the existing vegetation at the time of settlement was not well equilibrated with the associated physical environment and that this marked disequilibrium resulted in an increased opportunity for invasion and naturalization by new species fortuitously preadapted to the prevailing conditions. Many such species in the California Central Valley grassland should, perhaps, be considered 'new natives' because they exhibit a measure of ecological stability that ensures their continuance in face of the natural processes of vegetational change (Heady 1977). Today it is estimated that over 50% of the vegetational cover of 'native' (unimproved) rangeland in the Central Valley is made up of exotic species (Burchann 1957; Heady 1977). Introduced species such as wild oats (*Avena fatua* L.; Poaceae), soft brome (*Bromus mollis* L.; Poaceae), and filaree (*Erodium* spp.) are major contributors to rangeland productivity. Of course, others such as Klamath weed (*Hypericum perforatum* L.; Clusiaceae), medusahead (*Elymus caput-medusae* Boiss.; Poaceae), and goatgrass (*Aegilops triuncialis* L.; Poaceae) are considered rangeland weeds that reduce forage yield.

The current makeup of the California flora in terms of the introduced and native taxa show proportional differences according to rank in the classification hierarchy (Table 4). The number of introduced families is low (6.8%) in comparison to the number of introduced species (16.2%), and the number of introduced genera is high (24.8%). The high incidence of new introduced genera, around one-fourth of the total, suggests that the introduced taxa have phylogenies divergent enough from the native taxa to cause a substantial increase in the breadth of the biological diversity of the flora as a whole.

The over 1000 species of adventive and naturalized plants can further be generally divided into two types: (1) those that arrived by accident as contaminants of crop seed, etc.; and (2) those that were brought in intentionally for the purpose of being cultivated and escaped. This latter group of 'escapees' have been the focus of a special project being carried out by the California Native Plant Society (CNPS) over the past few years (Smith 1979). The project is directed at cataloging and evaluating escaped exotics with regard to the threat they might pose to native species through the process of competitive exclusion. The first list of 'escapees' compiled contained 326 species. Although most of the 326 were among the 1000 introduced species considered in the references mentioned above, 44 were not, and evidently represent recent naturalization supplying the ongoing invasion. The proportion of 'escapees' relative to the total number of cultivated species in California is not known since no accounting of the numerous kinds of plants (probably several thousand) grown in fields, orchards, aquaria, gardens and nurseries has been attempted. It should be supposed that, with the high commercial activity in gardening and landscaping and the large number of species involved, the flood of new exotics to the wilds will continue.

Table 4. Statistical summary of the vascular flora of California in terms of native and introduced taxa according to classification hierarchy. Figures in ( ) indicate number of California endemics in category (prepared from Smith and Noldeke 1960, Noldeke and Howell 1960 and Howell 1972 as based on Munz and Keck 1959 and of Munz 1968).

Taxonomic level recognized	No. native		No. introduced	Total no.	% introduced
Families	155		12	167	6.8
Genera	857	(29)	282	1139	24.8
Species	5027	(1510)	975	6002	16.2
Specific and subspecific	6658	(2633)	1017	7675	13.2

The documentation of exotics becoming adventive or naturalized is a much easier task than determining the degree of threat they might pose to native species. Evaluations by CNPS of the 326 escapees in this regard have been toward first identifying the most obvious offenders. The list of 326 was shrunk to 100, then to 37 and finally to 6 species that appear aggressive enough to assume dominance in certain areas of native vegetation. The final six are: *Cortaderia jubata* (Lem.) Stapf. (Poaceae) (Andean pampas grass); *Cytisus monspessulanus* L. (Papilionaceae) (French broom); *C. scoparius* (L.) Link (Scotch broom); *Ulex europaeus* L. (Papilionaceae) (gorse); *Carpobrotus edulis* (L.) Bolus. (Aizoaceae) (ice plant); and *Tamarix ramosissma* LEDEB. (Tamariaceae) (salt cedar). Information is being sought on other species. A threat to native species is presumed if roles of dominance are assumed by 'escapees', especially if their potential habitat includes those occupied by native species that are considered rare and/or endangered (E. McClintock, pers. comm.).

Another primary effort of CNPS has accordingly been devoted to identifying, mapping and evaluating the status of the less common or threatened native plants in the State (Smith *et al.* 1980). Presently, 1394 species and subspecies, more than $\frac{1}{4}$ of the natives, have been categorized under this designation. The group has been further characterized as follows: (1) those presumed extinct (list one, 44 species); (2) those rare and endangered (list two, 680 species); (3) those rare but not endangered (list three, 430 species); and (4) those rare in California but more widely distributed outside the State (list four, 240 species).

Those classified as 'presumed extinct' are of particular interest in this discussion since they represent probable examples of species removed from ecosystems. Since the list was last published in 1980 (2nd edition revised), 10 of the 44 species have been located alive in California, 6 have been determined to still exist in adjoining states or regions, 5 are described as subspecies of more generally occurring species and several others initially collected from remote locations are thought by specialists to have a high probability of still existing there. The case against any chance of recovery appears strong for about 6 species of the initial 44 presumed extinct (A. Howard, pers. comm.). In general none of the initial group were ever abundant, and most were known only from a single location and in some cases as a collection from one or two individual plants. In view of their beginning rarity it is unlikely that any of the probable extinct species ever played significant roles in the structure and function of the ecosystems of which they were/are a part. On the balance sheet of current species richness, one aspect of diversity, the probable six extinctions, is far overshadowed by the documented 1000 species introductions.

The plant species listed as endangered and/or rare (CNPS lists two and three, respectively) are also, as might be surmised from the designations, only minor structural components of the ecosystems where they occur. There is little indication that any were ever major components of any extensive vegetations. In particular it appears that essentially all those designated as endangered have always been rare. Most are endemic, probably of recent origin, i.e. neoendemics, that belong to genera and families that exhibit a high degree of evolutionary activity. Examples from lists two and three are: (1) members of the genus *Eriogonum* (Polygonaceae), 51 rare species and varieties out of approximately 104 species and 50 varieties in the flora; (2) the genus *Arctostaphalus* (Ericaceae), 37 species and subspecies out of approximately 43 species and 18 subspecies or varieties in the flora; and (3) the genus *Astragalus* (Leguminosae), 37 species and varieties out of approximately 94 species and 32 varieties in the flora. The pattern calls to mind discussions on speciation from years ago in graduate school at the New York Botanical Garden, during which I remember the noted field botanist, taxonomist and plant systematist, Arthur Cronquist, expressing the opinion that incipient species were constantly being 'spewed off' of established species and that most of these 'new species' failed to increase beyond one or a few individuals. The point is that field collectors must be discriminating to obtain specimens that are generally representative of successfully established populations. It seems probable that many of the species listed as rare are more or less on the fringe of successful establishment. In this regard, it is apparent that what taxonomists decide to call a species is of great significance.

The general ecological profile of the rare native species contrasts sharply with that of the naturalized exotics. The latter have already passed through the screen of successful establishment. In comparing the future potential of the two groups, the rare natives and the naturalized exotics, I audaciously opt for the latter as possessing qualities most suggestive of ecological significance and economic worth. This idea is related to Edgar Anderson's often cited hypothesis on the dump heap origin of Agriculture in which he suggested that weedy plants associated with rubbish piles (i.e. 'kitchen middens of fisher folk'), gave rise to the first and some of our most important domesticated crops (Anderson 1952). I am not aware of any established links between threats of extinction to natives and competition from naturalized exotics in California other than in theory although such cases are purported to have occurred in Australia (Bell 1983). At this juncture it appears that species have been more readily added than removed from the flora of highly industrialized California.

Biological Control and Ecosystem Structure and Function

Inadvertant Biological Control

The common objective in the biological control of weeds on rangeland is the reduction or removal of a targeted weed species through the action of an attacking organism. The introduction of attacking organisms for this purpose is customarily approached with great caution to avoid a mistake whereby non-target species are also attacked. The kinds of risks involved in introducing an attacker may be partly understood from results gleaned from some selected rather extensive 'experiments' that were performed inadvertently. Three such 'experiments', chestnut blight on American chestnut, Dutch elm disease on American elm and an unknown suspect on eastern hemlock will be briefly considered as 'worst case' scenarios.

The American chestnut (*Castanea dentata* [H. Marsh] Borkh.; Fagaceae) was until recently a dominant tree of the eastern deciduous forest of North America extending over a range of *c.* 80 million ha (200 million acres). It was a tree valued for lumber, fruit, chemicals (used in the leather tanning industry) and aesthetic appeal. In 1904, chestnut blight, a fungal pathogen (*Endothia parasitica* [Murr.] P.J. & H.W. And.; Sphaeriales), was discovered on chestnut trees in Bronx Park, New York City (Gravatt and Parker 1949). It proved to be highly lethal to mature tree stems. It spread rapidly and in < 50 yrs, 80% of the chestnut tree boles in the eastern deciduous forest were dead. This has been termed '... perhaps the greatest single natural catastrophe in the annals of forest history' (MacDonald *et al.* 1978). An appraisal of the current status of chestnut and its ecosystems is in order.

Granting the catastrophic dimensions of the American chestnut die off, it seems important to point out that the species has by no means been eliminated. It still persists over most of its original range albeit, in most instances, in a highly modified form. Chestnut sprouts vigorously from the base of the dead boles, and as such, it is now an understory shrub in many places where it once was a major component of the tree canopy. Data in a recent report by McCormick and Platt (1980) shows that in 1970 chestnut (stump sprouts) ranked seventh in IV (importance value) among 26 woody species of a forest in Virginia that was devastated by chestnut blight around 1920. Stump sprouts exhibit some juvenile resistance at first but then become susceptible to the blight and after persisting for a few years succumb once more to fungal infections; then they sprout again and so on indefinitely. Almost pure stands of chestnut resprouts are observed in some areas of West Virginia where present-day forests have been recently clearcut (M. Double, pers. comm.). The pattern of chestnut as an understory shrub is a common one throughout the deciduous forest region today.

Perhaps of equal, or maybe greater, significance is the survival of some large individual trees of *C. dentata* throughout the length and breadth of its original range. Living trees are reported from North Carolina on the south (Stambaugh and Nash 1982) to New York on the east (Dietz 1978) to Michigan on the northwest (Brewer 1982) and West Virginia in the middle (Given and Haynes 1978). Tree survival has been attributed to: (1) disjunct distributions, wherein isolation has permitted evasion of the blight; (2) resistance, wherein the trees are purported to be tolerant of the blight; and (3) blight hypovirulence, wherein the blight organism itself has been reduced in its pathogenicity. All three of these survival mechanisms, especially the latter, are currently being actively studied. Together they provide ample evidence of a resurgent interest and optimism in the prospect of restoring *C. dentata* to a place of prominence in the American landscape. Two symposia have recently been held on the subject after a long period of apparent discouragement and dwindling interest (MacDonald *et al.* 1978; Smith and MacDonald 1982).

A matter of relevance to biological control is that the blight fungus (*E. parasitica*) is not specific to chestnut but has been reported on some 24 other tree species in eastern North America, particularly oaks (16 species) (Stipes *et al.* 1978). It appears innocuous in most cases but is accorded a role in the decline of eastern live oak on the Atlantic seaboard, while another fungus (*Cephalosporium* sp.; Hyphomycetes) is associated with live oak decline in central Texas (Stipes *et al.* 1978).

The aftermath of chestnut blight on the total forest ecosystem has not been a dramatic long-term disruption of ecosystem functional processes. The immediate consequence of death of American chestnut was development of gaps or holes in the energy-accumulating forest canopy. Ecosystem 'goods' in terms of chestnut fruits (nuts) and available chestnut timber declined markedly. The spread of the disease was so rapid that the decrease was essentially synchronous over the eastern forest region. The demise of chestnut was followed by a surge of growth by associated species which closed the gaps and holes in the forest canopy in 10–20 yrs. Oaks (*Quercus* spp.) responded most quickly in the south, e.g. Tennessee and Virginia (Woods and Shanks 1959; McCormick and Platt 1980), and cherry birch (*B. lenta*) in the north, e.g. New Jersey and Connecticut (Good 1968; Davis 1981*b*). Through the years hickory (*Carya* spp.; Juglandaceae) has increased in the south to the point of codominance with oaks (McCormick and Platt 1980), while in the north, oaks have continued to increase at the expense of birch (Davis 1983*a*). Other forest tree species, e.g. maples (*Acer* spp.), ashes (*Fraxinus* spp.; Oleaceae) and birches (*Betula* spp.) have also undergone population changes in the blight areas, as elsewhere.

Although projection of 'recovery' to some presumed new climax is a common practice (Wood and Shanks 1959; McCormick and Platt 1980), the results must be viewed as illusionary if the expectation extends beyond the generation time of the longest lived dominants. After all, chestnut had occupied the forest in New York for a brief 2000 yrs before the blight struck (Fig. 3). Based on probable life history considerations, 2000 yrs is equivalent to only three or four generations, hardly enough cycles to establish much integration. Still the system as a whole does not appear erratic but regulated in terms of functional processes.

The functional stability of the eastern deciduous forest ecosystem is not dependent on a definite species composition but that the species comprising the system have the capacity for the performance of essential processes. In arguing a point similar to this, Slobodkin *et al.* (1967) noted that the demise of the American chestnut '... has not left holes in our forests' and that 'Not one mature chestnut can be put back without displacing plants of other species', i.e. the processes once performed by chestnut are now being carried out by other tree species. In terms of ecosystem 'goods and services', the 'goods' of oak, birch, beech, maple, etc., have been substituted for the 'goods' of chestnut, and the 'services' have remained about the same.

The Dutch elm disease (DED) 'worst case' number two may be of more international interest since it has been said to have '... created more worldwide environmental concern than any other tree disease' and '... has proven to be one of the most devastating tree diseases known to mankind' (Karnosky 1979). The case of the American elm, *Ulmus americana* L. (Ulmaceae), in relation to DED caused by the fungus, *Ceratocystis ulmi* (Buismam) C. Moreau (Microascales), is similar to the case presented for the American chestnut. *U. americana* was a major component of the eastern deciduous forest at the time of European settlement. It was particularly abundant in low-lying lands along streams and rivers throughout almost all of the deciduous forest region. In addition to being a major forest species, its stately appearance led to its being selected as a favored choice for shade tree plantings in cities and towns all across the country, especially in the northeast. It has been called 'nature's noblest vegetable' (Karnosky 1979).

DED was unwittingly introduced to North America around 1930. It was first reported from Ohio where it is believed to have arrived via diseased elm logs from Europe. Soon after it was found in New Jersey and New York (Karnosky 1979). By 1949 it was reported from natural forests and shade tree plantings from Massachusetts in the northeast to Virginia to the south and Indiana to the west (Swingle *et al.* 1949). Unlike the chestnut blight, its spread is closely tied to insects: four species of elm bark beetles (Coleoptera: Scolytidae), three introduced (*Scolytus multistriatus* [Marsh.], *S. scolytus* F., and *S. pygmaeus* F.) and one native (*Hylurgopinus rufipes* Eichhoff) act as vectors (Karnosky 1979). Shade trees planted in parks and lining streets of many northeastern cities and towns have been particularly devastated. In areas where the DED has struck, tree death estimates range from 75–95% of the elm population.

As in American chestnut, resprouting in American elm is prolific. Of course stump and root sprouts cannot be tolerated as substitutes for living trees in streetside plantings but they do have considerable significance in the continuance of the species as part of the forest ecosystem. After reviewing the literature for both Europe and America in this regard Karnosky (1979) concludes that 'millions of root-sprouts are now developing in the original outbreak area, indicating that elms will continue to inhabit much of their original range — but not as dominant components which they once were.' and further

> '... resprouting of diseased elms will ensure that elms will continue to be important components of forest stands in north-temperate regions around the world. Thus, the major environmental impact of DED on elm forests will be the community structure changes resulting from the remaining and persisting elms being shrubby, understory trees rather than the major overstory trees that their progenitors once were.'

American elm also continues to be perpetuated by seed. Young trees apparently possess an age-related resistance that allows them to reach seed bearing size even though the average life span is greatly reduced over predisease times. Older resistant individuals also persist, especially in mesic uplands (Richardson and Cares 1976). The opportunity for developing future resistant populations through genetic selection thus appears even more favorable for American elm than for American chestnut (Barnes 1976; Richardson and Cares 1976).

Five to ten yrs following the demise of canopy size American elm in deciduous swamp communities in Michigan, black ash (*Fraxinus nigra* H. Marsh.), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis* N.L. Britt.) became dominant in the tree layer and were expanding to fill the holes left by the dead elms (Barnes 1976). Twenty-six years after DED struck a mesic upland site in the same State, American elm still ranked first in importance value among forest trees but was declining relative to the oaks (*Quercus* spp.) and red maple (Richardson and Cares 1976). The rate of canopy hole closure was not indicated but this was implied to be proceeding.

In terms of ecosystem 'goods and services', the same kinds of trends as observed for the former chestnut forests are evident here though fewer data are available. The 'goods' are changing but the 'services' are remaining about the same.

The third 'worst case' concerns eastern hemlock (*T. canadensis*). Its story is less well known than that of American chestnut and American elm. It is an evergreen conifer that has exhibited a consistent association with deciduous trees through time (Table 2, Fig. 3). In parts of its range it forms almost pure stands and exhibits vigorous growth. Today there is no apparent unusual threat to hemlock's health. The case for hemlock involvement in a biological control episode is based on suggestive patterns in the pollen record (Davis 1981*b*, 1983*a*). Like other deciduous forest trees it migrated north after the last glaciation, but followed a distinctive northwesterly path (Fig. 3). About 5000 yrs ago it was widely represented as a major species in the regional vegetation. Then approximately 4800 yrs ago there was a sudden and large decrease in the rate of hemlock pollen deposition. The change appears synchronous throughout the entire deciduous forest. Pollen rain from other tree species remained high or increased. There was an immediate increase in birch pollen in the north followed by an increase in oak. In other parts of the range, pollen deposition rates increased for various combinations of beech, hickory, maple, oak and pine (Davis 1983*a*).

The decrease in deposition in hemlock pollen at the 4800-yr level and the subsequent compensating shifts in the pollen of associated species match closely the kinds of changes in chestnut pollen and the pollen of its associates in modern time as related to chestnut blight. This suggests strongly the involvement of some biological agent, possibly a pathogen or an insect, in the prehistoric demise of hemlock. It should be noted that hemlock did not disappear completely during this episode but remained at low levels for about 1000 yrs and then started to increase so that by about 3000 yrs B.P. it had returned to a position of major importance in the regional vegetation (Davis 1983*a*). Thus, here again in terms of ecosystem 'goods and services' the system appears to have regulated the 'goods' supply by substituting the 'goods' of other species for the 'goods' of hemlock while maintaining ecosystem processes or 'services' at a nearly constant level.

Biological Control of Weeds

A review of successful biological control programs fostered or carried out to remove undesirable plants on rangelands indicate results similar to the accidents or fortuitous case histories just discussed. Four selected examples, two representing native weeds, manuka (*Leptospermum scoparium* Forst.; Myrtaceae) in New Zealand and prickly pear (*Opuntia* spp.; Cactaceae) on Santa Cruz Island, California, and two representing introduced weeds, Klamath weed (*H. perforatum*) in northwestern North America and prickly pear (*Opuntia* spp.) in Australia and other places, will be briefly considered in this regard.

Manuka, a native shrub of New Zealand, is an aggressive invader of established grassland on both the North and South Islands. The acreage it occupies has greatly increased in historical times, particularly in areas cleared of forests to establish pastures. Estimates of hectares infested, 2.8 million on the North Island and 0.6 million on the South Island, amount to 25% and 4% of the respective island areas (Hoy 1961). Dense stands of manuka suppress production of associated grasses and herbs. Such infestations diminish forage yield and pose vegetation management problems (Sewell 1949). Biological control of manuka was considered as a possible remedy only after the chance introduction of the mealy bug, *Eriococcus orariensis* Hoy (Homoptera: Eriococcidae), from Australia was discovered on the South Island (Hoy 1949, 1961). *E. orariensis* was observed to be effective in killing infected plants over a period of years and acquired the designation 'manuka blight' (Sewell 1949). Starting in 1946 the use of manuka blight was popularized in newspapers and was advertised for sale to farmers in 1948 (Hoy 1961). Its spread was fostered by man on both the North and the South Island at least up through 1953. Thereafter opposition to its use developed from those who feared eradication of the target native plant and possible damage to the affected watersheds as a result of its elimination (Hoy 1961). Distribution of the mealy bug soon became essentially coincident with that of the host plant. Manuka die-off was striking throughout its entire range at first but diminished markedly in places, particularly the North Island, where the debilitating insect became parasitized by a fungus. In fact, Hoy (1961) concluded in this connection that 'the recovery of *L. scoparium* in the North Island has been as spectacular as the initial control achieved by *E. orariensis*'. The fungus had little affect in reducing the efficacy of the mealy bug on the drier South Island or in the drier parts of the North Island. Effective control of manuka continued to be observed in these drier areas up through 1960 (Hoy 1961). Concern over possible eradication of *L. scoparium* in New Zealand proved premature since its continuance in the moister portions of its range now seem assured.

A series of significant vegetation structural changes during the manuka episode are related to shifts in both the goods and services (processes) provided by the ecosystem. Forest trees were removed initially to increase grass forage production which, in turn, was suppressed by the invasion of native manuka shrubs, but restored when the shrubs were killed by the introduced manuka blight (changes in goods). Physiological processes of trees, shrubs and herbs are sufficiently different as to represent substantial shifts in ecosystem services as the dominant life form changed from one to another.

Two species of native prickly pear (*Opuntia littoralis* [Engelman] Cockerell and *O. oricola* Philbrick) on Santa Cruz Island, just off the coast of southern California, increased to pest proportions during the early part of this century. Beginning in the late 1930s biological control efforts were undertaken using native mainland *Opuntia* insects not found on the island (Goeden *et al.* 1957). Although introduction of several different insect genera was attempted, the primary success was attained with *Dactylopius opuntiae* Cockerell (Homoptera: Dactylopiidae), a cochineal insect from Mexico via Australia and Hawaii. After successful establishment of a strain of *D. opuntiae* in 1951, prickly pear decreased markedly in abundance and livestock grazing conditions improved greatly (Goeden *et al.* 1967; Goeden and Ricker 1981). However, scattered clumps of prickly pear are still found throughout the island and in some places in quantity (R.D. Goeden, pers. comm.). In recent years the prickly pear mortality rate has decreased which may in part be due to changes in capacity of *Dactylopius* to inflict damage since appearance of some of its predators on the island (R.D. Goeden, pers. comm.). The initial greater effectiveness of *D. opuntiae* in killing prickly pear on Santa Cruz Island as opposed to the adjacent mainland was largely ascribed to absence of cochineal insect predators in the island situation. Over the years there has been a shift in relative amounts of the two *Opuntia* species present in favor of *O. oricola*, which is less susceptible to damage by *Dactylopius*. Still, there appears to be little chance that either species will be eliminated from the island. Under current conditions prickly pear should be projected as a continuing conspicuous constituent of the vegetation.

The increase in density of native prickly pear to pest proportions and their latter demise is indicative of shifts in the goods and services provided by the ecosystem. Not only does it represent changes in vegetation structure due to the increase and decrease of different lifeforms but also alterations in the basic mode of photosynthetic production. Prickly pear exhibit crassulacean acid metabolism which has direct implications on how water and other plant growth resources from the environment are processed.

Klamath weed, or St. Johnswort (*H. perforatum*), a native of Europe and Asia, was introduced into the rangelands of northwestern North America in the early 1900s. It spread rapidly and by 1940 had become a prominent component of rangeland vegetation throughout an area covering an estimated 2 million ha (Goeden 1978). It was an undesirable addition to northwest rangelands because, besides being unpalatable, it exhibited certain toxicities to livestock (Huffaker and Holloway 1949). A perennial herb, it exhibited a particularly aggressive characteristic of not only invading new territory but of persisting indefinitely in the acquired spaces once gained. Affected areas could not be readily restored to productive status by conventional range vegetation management techniques.

Biological control efforts were undertaken in the early 1940s and by 1945 a leaf-feeding beetle (*Chrysolina quadrigemina* Suffrian; Coleoptera: Chrysomelidae), a native of France, that had been partially screened for biocontrol work in Australia, was, after further testing, released in northern California. The results were phenomenal. Within a decade the amount of Klamath weed was reduced an estimated 99% (Huffaker and Kennett 1959). The greatest influence of the leaf beetle appears to have been in the central area of the Klamath weed infestation. Weed populations toward the margins of its range northward in Canada and southward in California have been less affected.

The ecological position occupied by Klamath weed in the natural landscape changed under the influence of its insect predator from full-sun, open habitat to partial-shade understory habitat (Huffaker and Kennett 1959). It seems significant that the target species still persists throughout the range it attained during the period of its rapid invasion. Thus *H. perforatum* even in its reduced state is still more abundant than many native species in the flora. Its success should qualify it for the designation 'new native' since it now appears to be a permanent member of northwestern rangeland vegetation even in the presence of its imported enemies and the competition of associated plant species. The initial invasion of Klamath weed brought about a change in the specific goods and services provided by the ecosystem. Structural changes, though not as great as for manuka and prickly pear (see above), were associated with a shift in the quality of herbaceous plants for grazing. Klamath weed, an undesirable perennial forb, tended to replace more desirable grasses. The introduction of exotic insects for biological control reduced Klamath weed and shifted goods and services back toward grass goods and grass processes.

Biological control of prickly pear in Australia must be the most publicized biological control episode ever carried out. It is a favored example of the biological control concept used in biology textbooks as well as in technical publications of related fields (Heady

1975). The principal organisms involved are two closely related species or varieties of prickly pear, *Opuntia inermis* (DC.) DC. and *O. stricta* (Haworth) Haworth from the Gulf Coast in North America, and the moth *Cactoblastis cactorum* (Berg.) (Lepidoptera: Pyralidae) from Argentina in South America (Dodd 1940; Mann 1970). The campaign against prickly pear was undertaken in response to an enormous and alarming infestation that occurred about the turn of the century. The major pest species were brought into Australia between the early and mid-1800s. They were grown as hedges and were distributed widely for that purpose from about 1840–70. Their ability to spread naturally started to cause serious apprehension in the 1880s. By 1900 an estimated 4 million ha were affected. Following a serious drought in 1902 in which prickly pear was 'freely fed' to livestock the invasion rate accelerated. At its peak in 1925 it was estimated that an area of 24 million ha had been invaded and that the rate of spread was *c.* 0.5 million ha/yr (Dodd 1940). In 1925 *C. cactorum* was successfully introduced and started to be distributed through the infected area. Results of the insect killing the cactus were dramatic and Dodd (1940) indicates that after the first three years (i.e. in 1928), it was evident that prickly pear would be controlled. Most of the large pure stands of the pest prickly pears were effectively reduced to scattered plants as he predicted. *C. cactorum* continues to be effective in controlling *O. inermis* and *O. stricta* population levels in much of the area. It is significant, however, that the pest prickly pears still persist throughout most of the area they once dominated (Mann 1970; White 1981) and that they are still spreading, albeit at a slower rate (Haseler 1981). Haseler also points out that satisfactory control was never realized in central and southern New South Wales or coastal Queensland. The evidence suggests that prickly pear is well enough suited to the physical and biotic environments of Australia to persist indefinitely as a part of natural spontaneous vegetation. Perhaps it is a 'new native'. Changes in ecosystem goods and services in the case of invasion and control of prickly pear in Australia are obvious in terms of changes that took place in physiognomic structure and physiological processes, and parallel quite closely to those noted for Santa Cruz Island. A difference stands out in that prickly pear and its associated fauna have now established a new place in the Australian landscape as has Klamath weed in northwestern North America.

Australia is just one of a number of places where biological control efforts on various species of prickly pear using insect enemies has been declared a success (Table 5). In none of the instances examined does it appear that weedy prickly pears, foreign or native, have been eliminated through biological control. In fact no instance has been found in which biological control, either purposeful or accidental, has eliminated a plant species completely. The reoccurring suggestion that this might be the case for *Tribulus cistoides* L. (Zygophyllaceae) in Hawaii is in error (G. Funasaki, pers. comm.), although in animals such a case has recently been reported for an endemic snail on Moorea, an island in French Polynesia (Clarke *et al.* 1984). That is not to say that it has not occurred for plants. It probably has in view of all the plant species that have gone extinct in the past. But historical evidence suggests that the likelihood of a predator insect bringing about extinction of a plant host successful enough to be labelled 'weed' is quite remote; i.e. low risk.

Discussion and Conclusions

Now what does all the above have to do with applied ecology, and more specifically biological control of weeds on rangelands, as intimated in the introduction? It is simply this. The picture of vegetation dynamics that emerges from information presented on

Table 5. Summary of selected successful biological control efforts of prickly pear from different parts of the world using *Dactylopius* spp. and *Cactoblastis cactorum* (Berg.) (from Goeden 1978).

Opuntia species	Location	Insect species	Results[1]	Weed status[2]
O. aurantiaca Lindley	Australia	*Dactylopius* spp.	Good	Low density
O. aurantiaca	South Africa	*Dactylopius* spp. and *C. cactorum*	Poor	Pest levels
O. dillenii (Ker-Gaw.) Haw.	India and Ceylon	*D. opuntiae* (Cockerell)	Good	Low density
O. elatior Miller	India and Ceylon	*D. opuntiae*	Fair	Common
O. elatior	Celebes	*D. opuntiae*	Good	Low density
O. imbricata (Haw.) DC.	Australia	*D. newsteadii* Cock.	Good	Low density
O. inermis DC.	Australia	*C. cactorum*	Good	Low density
O. littoralis (Eng.) Cock.	Santa Cruz Is., USA	*D. opuntiae*	Good	Low density
O. megacantha Salm-Dyck	Hawaii	*C. cactorum*	Fair[3]	Low density
O. megacantha	Hawaii	*D. opuntiae*	Fair[4]	Low density
O. megacantha	South Africa	*D. opuntiae* (*C. cactorum*)	Good	Low density
O. oricola Philb.	Santa Cruz Is., USA	*D. opuntiae*	Fair	Low density[5]
O. streptacantha Lemaire	Australia	*D. opuntiae*	Partial	?
O. tomentosa Salm-Dyck	Australia	*D. opuntiae*	Good	Low density
O. triacantha (Will.) Sweet	LeeWard Is.	*C. cactorum*	Good	Low density
O. tuna (L.) Miller	Mauritius	*C. cactorum* then *D. opuntiae*	Good	Low density
O. vulgaris Miller	India–Ceylon	*D. ceylonicus* (Green)	Good	Low density
O. vulgaris	Australia	*D. ceylonicus*	Good	Low density
O. vulgaris	South Africa	*D. ceylonicus*	Good	Low density

[1] Usually judged relative to the degree of reduction in places of highest infestations — results may differ in other parts of range.

[2] Relative to abundance attained during height of infestation.

[3] Effective in intermediate elevational range of infestation.

[4] Effective in lower elevational range of infestation.

[5] Relatively more resistant and abundant than the associated *O. littoralis*.

creosotebush and creosotebush deserts, eastern deciduous forests, tropical forests, California floristics and episodes of biological control, is strikingly different from that which is commonly envisioned by many, if not most, practitioners of vegetation management, including those who would be such by employing or withholding biological control. The contrast to the seemingly ubiquitous, Clementsian climax (super organism — ancient in age — all parts essential — delicately balanced) view is that: (1) natural vegetation systems reviewed here exhibit ongoing change in species composition in time and space, i.e. both paleoecological and historical data show that plant communities are continually being assembled and reassembled in terms of species makeups; (2) vegetation (ecosystem) stability factors are more associated with physiognomy and functional processes than species persistence; (3) the flux rate in major plant species has been too fast to allow for the myriad of generations usually postulated as necessary for the refined development of co-evolutionarily integrated, biologically regulated and delicately balanced ecosystems of landscape scale; (4) some systems appear highly susceptible to invasion by introduced species, which then persist as major fluctuating components of the vegetation; and (5) the relative importance of species in ecosystems can be changed markedly and quickly by biological control type agents.

The meaning of vegetation dynamics as just summarized in relation to the specific query, 'should exotic insects (or other exotic biological agents) be used to control weedy native plants?' is that this individualistic view which the data presented supports tends to minimize or negate the concerns giving rise to the questions in the first place; i.e. the collapse of ecosystems is not an imminent prospect of biological control. Even in the case of dominant species being decimated by exotic biological agents, as in the examples of chestnut, elm, and perhaps hemlock, the ecosystem appeared to adjust rapidly in restoring productive capacity and functional processes. This is not to say that the short-term effects of biotic agents are not dramatic from a societal point of view, as was clearly the case for chestnut, where emotional and aesthetic attachments are evidently stronger for chestnut than for the ecosystem of which it is a part. In cases like this, the point of concern should be clearly identified and not generally perceived as a whole ecosystem disaster.

I conclude that:

(1) The sanctity attributed to 'climax vegetation' because it is 'ancient in age' and 'stable in species composition' is without merit. The label 'native' does not make a species sacrosanct. Clearly the status of nativity for plant species making up today's natural vegetation is relative (Figs. 1, 2; Tables 1, 2).

(2) Plants that are behaving as weeds on rangeland, whether designated native or introduced, obey similar principles as exemplified by manuka in New Zealand, Klamath weed in North America, and prickly pear in Australia, Santa Cruz Island and elsewhere.

(3) The chance of causing extinction of weedy plant species (either native or introduced) through the introduction of biological control agents is nil. The threat to non-target rare plant species needs to be evaluated on a case-by-case basis, but because of the minor role such plants play in the ecosystem any possible effect would be small at the ecosystem level.

(4) Biotic agents may rapidly alter prevalence of specific plant species without significantly affecting long-term structural and functional characteristics of the ecosystem, as with chestnut blight on American chestnut and Dutch elm disease on American elm, or conversely they may cause substantial shifts in both structure and function (goods and services), as found with *C. cactorum* and *Dactylopius* spp. on prickly pear, *C. quadrigemina* on Klamath weed and *E. orariensis* on manuka.

(5) The approach used in classical biological control provides a viable option for reducing undesirable plant species, introduced or native, that are interfering with the productivity of more desirable plants on rangelands. Contrary to a common assumption that the dominance of undesirable plants on rangelands always serve as evidence of overgrazing by livestock and that a reduction in grazing pressure will result in the reduction of the undesirable species, the evidence presented indicates that other environmental and biological factors weigh heavily in determining vegetation composition. Indeed, Harris (*in press*) contends that pure or nearly pure plant stands, whether native or introduced, are indicative of low herbivore pressure and that the introduction of appropriate insect herbivores will result in the decrease of dominance and an increase in plant species diversity.

The individual roles played by chestnut, elm, hemlock, manuka, Klamath weed, and prickly pear in their respective ecosystems were greatly altered through the action of biotic agents. Similar responses should be expected from purposeful biological control efforts directed at dominant native weed species like creosotebush and mesquite. After all, the whole intent of a biological control effort would be to bring about a notable shift in productive capacity and functional processes toward more favored species. Furthermore, if a species, native or non-native, is identified as a weed problem it may be assumed to be acting in an expansive mode that if not checked will result in ecosystem changes equal in magnitude but opposite in direction to those deemed desirable. The question as to whether or not biological control should be used in any given case seems to hinge mostly on the results of an evaluation of the positive and negative attributes of the weed itself and not on fears of postulated dire consequences to the ecosystem. This assumes of course that appropriate care is exercised in: (1) screening the designated biocontrol agent(s) for specificity, to prevent the decimation of some other species of high value; and (2) establishing reasonable assurance that the decrease in the target will result in an increase of more desirable species.

I realize that more basic philosophical questions are involved in the matters under consideration than has yet been alluded to. It goes to the heart of the question as to what man's place in nature is. Some question his right and capacity to manipulate the 'natural environment'. Nevertheless, the role man has played in contributing to dynamic change in vegetation has been on a grand scale and is of unquestionable significance. It is doubtful if there is a patch of vegetation on earth that does not bear some imprint of man's influence. Whether this is good or bad is a matter of both perspective and of the specific results realized. I fear that the viewpoint I have presented on the dynamics of natural vegetation may be misunderstood as support for disregarding ecological considerations. This is not intended, but instead, is meant to underscore the importance of relating theory and facts. Dr. Frank Egler (1984), a respected critic of contemporary plant ecology and a nemesis of traditional climax–successional theory, in speaking out for the Idea, and great value, of Natural Areas (i.e. areas of various sizes kept as free as possible from human influence) includes some salient comments in relation to vegetation dynamics and how man fits into the picture:

> '... I add a few comments about an Idea which has been understandably underplayed in Europe and Mediterranea, where man has man-handled the entire landscape for at least ten millenia; and underplayed in the Americas, where the pre-European Indian-influenced landscape has always been considered to be 'pristine,' 'virgin,' or 'climax.' It is also underconceived by those who consider the landscape of our hunter-gatherer ancestors of a million years ago to be 'natural'. (A hungry hunter-gatherer, territorially limited, will eat the last bulb or the last

> live meat, even as a hungry sailor ate the last dodo, all blissfully unaware of Rare and Endangered Species.) And the idea is underconceived by the present fashionableness of the preservationists, despite the extraordinary worthiness of all their accomplishments to date. They have preserved, too often with no interest in further knowledge of the changing nature of what they have preserved, at the highest level of holistic integration of that Nature.' ...
>
> 'A Natural Area, be it one hectare or a million hectares, is thus a control, a standard, a common denominator, essentially a non-human area, which by comparison with all managed areas, urban, farm, forest, and range, allows us to judge and separate the role of man himself in the man-and-his-total-environment ecosystem. It is not to be supposed that a Natural Area can be entirely free of the influence of man. Air pollution and winds, water pollution and aquifers and streams, and all the past influences of man leave their fingerprints and their footprints. But without Natural Areas, used by man, we have no logical grounds for evaluating the influence of man. Nor should we emotionally assume that Natural Areas are always bigger, better, finer, more Edenesque, and more ideal than what man has done. Man-less nature never did produce the ethics, the esthetics and the logic of a civilization.'

The above quote is not intended to shift our emphasis from vegetation dynamics to an augment for natural areas but to demonstrate that even in the ecology conservation enterprise of establishing natural areas the reality of vegetation interplay needs to be recognized. The impact of man has continued to increase through time. He now ranks as a primary force in shaping the environments of the globe and should be recognized in that context (Naveh and Lieberman 1984).

We must now be bold enough to accept the challenge of shaping and synthesizing new ecosystems even in the 'natural' environment. We can improve on nature with the guidance of what we can learn, or have learned, from Natural Areas. Biological control is one of the tools that needs to be employed. The structuring and restructuring of ecosystems will involve the visualization of appropriate arrangements of functional processes in time and space. Suites of plant species exhibiting the needed physiognomical, phenological, physiological, and phytosociological characteristics would need to be mixed with the appropriate microbes, invertebrates and higher animals. This is not an easy task, especially in light of present traditions and practices. An important step in this direction can be taken through more careful utilization of current information and theory on the dynamics of today's natural vegetation. Whether a correct single, simple theory on vegetation dynamics will be developed or not is open to question. What is clear is that many of the ideas associated with the species-constant climax concept are incorrect. The popular perception of balance in nature is a damnable heresy that persists in most fields of applied ecology and resource management to the detriment of establishing realistic goals and guides. It has been and is the basis for the formulation of much environmental policy and law, as can be attested to by many charged with meeting mitigation stipulations specified for environmental impact statements and/or regulations for inventorying natural biological resources. This socio-political involvement tends to make the task ahead more difficult but also more challenging.

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Depression in Ragwort (*Senecio jacobaea*) Abundance Following Introduction of *Tyria jacobaeae* and *Longitarsus jacobaeae* on the Central Coast of Oregon

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Abstract

This study measured the depression in abundance of dormant and actively growing stages of ragwort (*Senecio jacobaea*) following introduction of two phytophagous insects, ragwort flea beetle (*Longitarsus jacobaeae*) and cinnabar moth (*Tyria jacobaeae*) on the central coast of Oregon, U.S.A. Actively growing stages (seedlings, rosettes, flowering plants) declined to 3% and dormant stages (seeds and vegetative buds) declined to 32% of their former abundance following increase in herbivore populations. Based on evidence that the ragwort population was closed to migration, the depression in host abundance was ascribed to a >95% mortality spread over all actively growing stages followed by a 33% decline in per capita birth rate of the surviving reproductive plants. A decrease in ragwort standing crop was balanced by an increase in standing crop of other plant species (88% perennial grasses), leading to no net change in standing crop of the plant community. Two years following the decline, ragwort standing crop has remained at low levels (flowering plants have disappeared altogether), but densities of seedlings and small rosettes have rebounded to previous levels due to recruitment from the dormant seeds in the soil. Further study is required to determine whether ragwort will remain at low levels in the long term.

Réduction de l'Abondance des Séneçons Jacobée (*Senecio jacobaea*) Après l'Introduction du Lépidoptère Tyria (*Tyria jacobaeae*) et de l'Altise du Séneçon (*Longitarsus jacobaeae*)

Cette étude visait à mesurer la réduction de la densité des séneçons *Senecio jacobaea* (parties souterraines et aériennes) après l'introduction de deux insectes phytophages, soit l'altise *Longitarsus jacobaeae* et le lépidoptère *Tyria jacobaeae*, dans la partie centrale de la côte de l'Orégon aux États-Unis. La réduction a été exprimée selon la formule $q = N^*/K$, où K représente l'abondance moyenne de la plante hôte avent l'introduction des herbivores et N^* désigne le nombre réduit d'hôtes, cet équilibre étant probablement assuré par les herbivores. La valeur de q pour les parties aériennes (jeunes plants, rosettes, plantes à fleurs) était de 0,03 et de 0,32 pour les parties souterraines (graines et pousses). En se fondant sur des données selon lesquelles il n'y avait aucune migration des séneçons et que leur distribution aux différents stades de croissance était stable, le réduction du nombre d'hôtes a été attribuée à la baisse du taux de reproduction, plutôt qu'aux modifications des taux de survie ou de migration. La réduction du stock existant de séneçon a été équilibrée par une augmentation du stock existant d'autres espèces de plantes (herbes vivaces dans 98% des cas), ce qui n'a provoqué aucun changement net du stock existant de la communauté de plantes.

Introduction

The aim of biological control introductions is to depress host densities below an economic threshold and maintain them there. Hence we are concerned with two dynamic elements: (1) the level of depression in the host caused by the observed level of herbivory; and (2) the stability of the interaction over the long term. I studied depression and stability in ragwort (*Senecio jacobaea* L.; Compositae) abundance following introduction of cinnabar moth (*Tyria jacobaeae* [L.]; Lepidoptera: Arctiidae) and ragwort flea beetle (*Longitarsus jacobaeae* [Waterhouse]; Coleoptera: Chrysomelidae) on the central coast of Oregon, U.S.A.

The role of herbivores in depressing host abundance was evaluated from observations establishing: (1) an association, evidenced by negative correlation of insect and plant density; (2) a contact, evidenced by herbivore damage to the plants; and (3) a mechanism for population changes, expressed as changes in migration, birth, or death rates. I propose experiments to confirm relations of cause and effect suggested by my observational studies.

Organisms Studied

Ragwort is a biennial or short-lived perennial introduced to North America from Europe. It causes economic losses by poisoning cattle, horses, and swine (Muth 1968) and by displacing desirable forage. Ragwort was first recorded in western North Aermica in 1913 from Vancouver Island (Harris *et al.* 1971) and first recorded in Oregon in 1922 from Portland (Isaacson 1971). The weed now ranges from northwestern California to British Columbia from the coastline to the Cascade Mountains and beyond, with scattered reports having been confirmed from the Blue and Wallowa Mountains (D. Sharratt, OR State Dept. Agric., pers. comm.).

The cinnabar moth was introduced as a biological control agent from France and released near Fort Bragg, California, in 1959 (Hawkes 1968) and near Jordan (Linn County) and Valley Junction (Polk County), Oregon in 1960 (Isaacson 1971). The biology of the cinnabar moth has been reviewed by Dempster (1982). Adult moths emerge in late spring from overwintering pupae, and lay eggs in clusters on undersides of basal leaves of the ragwort food plant. Some plants are colonized by ovipositing adults, and others are colonized by immigrant larvae leaving defoliated hosts. Larvae can strip the flowering shoot to a bare stem, removing all the leaves and flowering heads. This rarely kills the plant, and in Oregon, regrowth shoots develop in autumn after larvae have entered the overwintering pupal stage.

The ragwort flea beetle was introduced from Italy and released in California near Fort Bragg in 1969 (Frick 1970*b*; Frick and Johnson 1973; Hawkes and Johnson 1978) and in Oregon near Trask River (Tillamook County) in 1971 and near Salem (Marion County) in 1972 (Isaacson 1978). The life history is described by Newton (1933), Frick (1970*a*, *b*, 1971) and Frick and Johnson (1972, 1973). Adults of the Italian biotype aestivate in summer, and resume activity in autumn when they mate and feed on foliage. Adults are pit feeders, rasping holes in the leaves of seedlings and rosettes. Eggs are laid singly on the plant or adjacent soil and larvae tunnel in leaves, petioles, stems and roots during winter and early spring. Pupation occurs in the soil and adults emerge in early summer.

Natural dispersal and deliberate redistribution have resulted in establishment of populations of both insects over nearly all of Oregon west of the Cascades.

Methods and Materials

The study was conducted in an abandoned pasture (Three Rocks Road South, 45°2′2″N., 123°58′42″E.) last grazed by dairy cattle in 1977. The site is part of the 3951 ha Cascade Head Scenic Research Area (CHSRA), which lies in Lincoln and Tillamook counties on the central coast of Oregon.

A total of 6505 flea beetle adults and 7000 cinnabar moth larvae were introduced to CHSRA (Table 1). These totals include local releases at Three Rocks Road Pasture of 2000 cinnabar moths in 1978, 220 flea beetles in 1979, and 485 flea beetles in 1980. All releases were made by the Oregon State Department of Agriculture and cooperators.

I began monitoring plant and insect populations in 1981. No quantitative estimates were made of insect density in 1981–82 because qualitative surveys revealed very few insects. In 1983, insect density was estimated in late summer from counts of cinnabar moth pupae and flea beetle adults in $\frac{1}{4}$ m^2 quadrats located at random. The percent of generative stems damaged by cinnabar moth and the level of damage to each stem was estimated each year 1981–83. In 1984, generative plants had disappeared so I evaluated cinnabar moth damage to vegetative plants. I made no assessment of damage by the flea beetle.

Table 1. Timing, size, and location of insect releases in Cascade Head Scenic Research Area, Oregon.

Year	Number of Individuals	Location	Ownership
a. *Longitarsus jacobaeae* (Waterhouse) releases.			
1976	750	6S,11W,Sec 14 SW	Nature Conservancy
1979	250	6S,11W,Sec 23 NE	U.S. Forest Service
1979	220	6S,11W,Sec 24 SW[1]	U.S. Forest Service
1980	485	6S,11W,Sec 24 SW[1]	U.S. Forest Service
1980	3000	6S,11W,Sec 23 NE	U.S. Forest Service
1982	2000	6S,11W,Sec 19	Private
b. *Tyria jacobaeae* (L.) releases.			
1978	1000	6S,11W,Sec 14	U.S. Forest Service
1978	2000	6S,11W,Sec 24 SE/SW[1]	U.S. Forest Service
1978	1000	6S,11W,Sec 13 NW/NE	Private
1978	1000	6S,11W,Sec 24 NW	Private
1978	1000	6S,11W,Sec 14 SW/NW	Nature Conservancy
1978	1000	6S,11W,Sec 14	Private

[1] Three Rocks Road Pasture.

Ragwort individuals were classified by stage: dormant seeds and vegetative buds in the soil, small vegetative plants (avg. dia. or $\frac{1}{2}$ [length + width] <7.5 cm), large vegetative plants (avg. dia. >7.5 cm), and generative plants.

Densities of dormant stages in the soil were estimated annually 1982–84 from soil cores 5 cm dia. and 10 cm deep. Soil cores were spread in a thin layer over sterilized potting soil in the greenhouse, watered daily, and the seeds allowed to germinate and vegetative buds allowed to sprout. Plantlets from seed were distinguished by symmetrical cotyledons and fine, fleshy, tapered taproots, while plantlets from vegetative buds on root fragments had asymmetrical leaves and stout, irregular root stocks.

The densities of actively growing stages were estimated each summer 1981–84 from $\frac{1}{4}$ m^2 quadrats. Counts of stems were transformed to counts of individuals by dividing by 3.55, the mean number of stems (ramets)/plant (genet) in a random sample of 64 ragwort plants taken in 1977, assuming that the mean number of ramets/genet did not change in the population from year to year.

Differences in plant density and dry mass among years were tested using the Kruskall-Wallis ANOVA by ranks. Pairwise comparisons between years were made using a nonparametric STP procedure based on the Mann-Whitney U Test (Sokal and Rohlf 1981). The samples sizes were randomly reduced to the minimum for groups compared for purposes of the test, which requires equal sample sizes. Means were estimated from full samples.

Results and Discussion

Herbivore Dynamics

The herbivores multiplied slowly at first. The cinnabar moth population remained at low levels through 1981–82, causing minor damage to 2% of 211 flowering stems sampled in the two years. In 1983, four years after release of the moth, the population erupted, causing major damage to 98% of the 92 flowering stems sampled, stripping them of their leaves and flower heads. In September 1983, cinnabar moth density averaged 2.4 (0–12) pupae/m^2. The flea beetle population erupted after summer 1982, reaching an average density of 5.6 (0–16) adults/m^2 in September 1983.

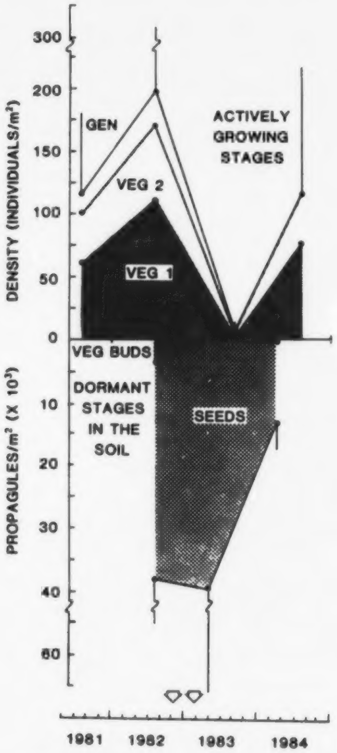

Fig. 1. Annual estimates of mean density (individuals/m^2) for dormant (vegetative buds and seeds) and actively growing stages (gen = generative plants, veg 2 = large vegetative plants, veg 1 = small vegetative plants) of ragwort population at Three Rocks Road pasture. Bars represent standard deviations. Sample sizes from left to right: actively growing stages (10, 10, 20, 10), dormant stages in soil (7, 13, 20). Arrows along time axis indicate approximate dates of insect outbreaks.

Host Dynamics

During 1981–82, ragwort's absolute and relative abundances were unchanging and extremely high. The combined density of actively growing stages averaged 157.2 plants/m^2 (Fig. 1). The distribution of density among stages was pyramidal; the percent of individuals in each actively growing stage declined in the series: small vegetative plants (54%), large vegetative plants (32%), generative plants (14%). Over 99% of individuals in the population were dormant propagules in the soil. In greenhouse experiments, 91–99% of the recruits were from seed, the remainder from vegetative buds. The combined dry mass of actively growing ragwort stages averaged 580.6 g/m^2 (Fig. 2); ragwort accounted for 72% of the above-ground dry mass of the plant community. The distribution of dry mass among stages was inversely pyramidal; the percent of total dry mass in each stage increased in the series: small vegetative plants (<1%), large vegetative plants (4%), and generative plants (95%).

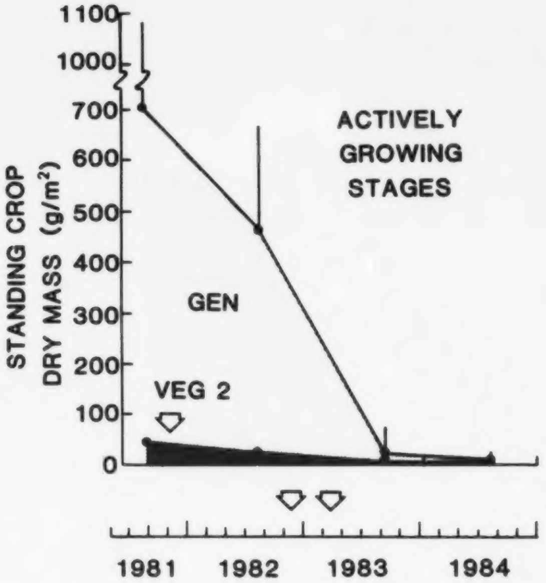

Fig. 2. Annual estimates of standing crop (dry g/m^2) for actively growing ragwort stages at Three Rocks Road Pasture. Means for the dry mass of small vegetative plants (2.3, 1.6, 0.04, 0.63 g/m^2 for 1981–84) were too small to graph. Bars represent standard deviations. Samples sizes listed in Fig. 1.

Accompanying the outbreak of herbivores in 1982–83 the plant community underwent dramatic changes. All stages of ragwort declined significantly. Above ground, the total density and total dry mass of stages declined to 3% of 1981–82 levels (Figs. 1 and 2). Comparing 1981 and 1984 populations, a 110-fold, 696 dry g/m^2 decline in ragwort standing crop was balanced by a 10-fold, 707 dry g/m^2 increase in standing crop of other species, leading to no net change in mean standing crop of the plant community. Perennial grasses accounted for 88% of the standing dry mass of other species in the new community. Below ground, the total density of ragwort propagules declined to 32% of 1982–83 levels (Fig. 2). Composition of the propagule bank changed as vegetative buds from root fragments declined to undetectable levels, suggesting they have a far shorter longevity in the soil than seeds.

To determine the mechanism for ragwort population decline, I evaluated the relative contribution of changes in rates of birth, death, and migration to changes in ragwort abundance. Here I summarize these findings, as they are to be reported in full detail elsewhere. Migration contributed very little to changes in local abundance. In mark-recapture experiments on wind-dispersed achenes, my co-worker Caroline Cox, and I have found dispersal distances are very short. For example, of 280,000 achenes marked, 31% travelled only 1 m, 89% travelled <5 m, and none travelled >14 m from the source plant. These findings suggest the population is effectively closed to migration, and we can look to changes in birth or death rates to explain local dynamics in the host population. The decline in the ragwort population was caused by >95% mortality spread evenly over actively growing stages followed by a 33% decline in the per capita birth rate of the surviving reproductive plants.

Long-term Stability

Further study is required to determine whether the ragwort population will remain at low levels. Ragwort relative abundance expressed as a percent of community standing crop remained at very low levels in 1983 (2.3%) and 1984 (0.8%). There were no generative plants in 1984, but very small vegetative plants rebounded to former levels due to recruitment from seed lying dormant in soil (Fig. 1). If herbivore pressure remains high, these small plants may grow to a size at which they become attacked by the insects and control will be maintained. On the other hand, reduction in herbivore populations by mortality or emigration may release the plant from control.

A Strategy for Biological Control

Findings in Oregon suggest a combination of agents which differ in the ways they exploit the host can be more effective in depressing host abundance than a single agent acting alone. Liberated from restraining mortalities in Oregon, the cinnabar moth has the capacity to locate all or nearly all the generative plants in a population and strip them to bare stems. The moth is strictly univoltine, and the inedible stems and roots left behind regenerate foliage and flowers in autumn after the moth has pupated. Thus damage is reduced by a portion of the plant being inedible, and compensatory growth and reproduction when the probability of encounter is low. The flea beetle consumes parts which are inedible to the cinnabar moth (petioles, stems, and roots) during seasons (autumn, winter) when the feeding stages of the cinnabar moth do not encounter the plant. Spreading herbivore pressure out in space and time may depress equilibrium levels of the host by reducing 'escapes' from herbivory.

Observational vs. Experimental Studies

Biological control introductions, including those made in this study, are rarely conducted as experimental tests of a herbivore treatment effect to which inferential statistics can be applied. Yet the effects of herbivores in depressing the host and maintaining it at low levels have been convincingly demonstrated by successful cases of biological control. In cases of marginal control, results could be made clearer and the conclusions firmer by experiments incorporating controls (designating treated and untreated systems), replication (using several systems for control and several for treatment), randomization (separating the subject systems into two groups by a random process), and interspersion of treated and untreated systems. I envision two kinds of experiments. First, the experiment could be imposed at the time agents are released. One difficulty with this approach is that migration of the insects will tend to compromise the independence of experimental units. Another difficulty is that establishment, in the present state of the art of biological control, is unpredictable. To enhance chances of success, it is perhaps a better expenditure of limited resources to make releases and follow up on those that become established, rather than conduct experiments at the establishment phase. A second kind of experiment could be performed after agents are established and appear to be affecting the host by: (1) deliberate increase in weed density; and (2) deliberate decrease or removal of herbivore populations. This would be an ideal follow-up to my observational study of population changes at Three Rocks Road pasture.

Conclusions

1. Acting alone, the cinnabar moth has not yielded strong depression in ragwort density in Oregon. In contrast, a combination of the cinnabar moth larvae attacking shoots in summer and flea beetle larvae attacking petioles, stems and roots in winter has yielded a 110-fold depression in ragwort standing crop at Cascade Head, Oregon. A similar strong depression in the ragwort abundance occurred near Fort Bragg, California, where ragwort flea beetle combined with the cinnabar moth reduced plant density from 71 rosettes/m^2 to 0.6 rosettes/m^2 in a period of four years (Hawkes and Johnson 1976).

2. In most weed populations, the number of individuals present as dormant propagules vastly exceeds the numbers present as growing plants. My findings suggest dormant seeds in the soil may allow regeneration of the plant population decimated by herbivores.

3. The role of biological agents in the control of host plant populations could be effectively demonstrated by showing: (a) host maintains high densities in absence of herbivores; (b) herbivores depress host density to low levels; (c) host is maintained at low densities by herbivores; and (d) host returns to high densities when released from herbivores. Observations made before and after introduction of the agents can provide evidence bearing on these propositions by establishing: (1) an association, evidenced by negative correlation of herbivore and plant density; (2) contact, evidenced by herbivore damage to the plants; and (3) a mechanism for population changes, expressed as changes in migration, birth, or death rates. My findings illustrate high ragwort levels in the absence of herbivores and a depression to low levels following herbivore increase due to >95% mortality spread over all actively growing ragwort stages. It remains to evaluate the long-term stability of the interaction between host and insects.

4. The validity of ascribing strong and stable depression in host abundance to changes in the activity of herbivores can be challenged since rarely do we know what the behaviour of the system would have been without herbivores. Experiments imposed on established populations by artificially increasing plant density and artificially decreasing herbivore density appear to be the most promising ways to answer this challenge.

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The Silwood International Project on the Biological Control of Weeds

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Abstract

A summary is given of objectives, methods and progress in a collaborative venture based at Silwood Park in England. The project was founded on the information provided by Julien (1982) in his catalogue *Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds* and this information has been substantially extended and elaborated through questionnaires completed by biocontrol practitioners in many parts of the world. Currently, the accumulated computer database comprises over 75 000 pieces of information from 627 attempted introductions. This provides a source of material for project participants in their analyses of factors relevant to the theory, practice and success of biological control of terrestrial weeds.

Projet International de Lutte Biologique Contre les Plantes Nuisibles à Silwood

Le présent rapport résume les objectifs et les méthodes d'un projet coopératif de lutte biologique contre les plantes nuisibles mis en oeuvre au parc Silwood en Angleterre, ainsi que les progrès réalisés. Ce projet repose sur les renseignements fournis par Julien (1982) dans l'ouvrage intitulé: '*Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds*', ainsi que sur les données rassemblées au moyen de questionnaires distribués à des praticiens de la lutte biologique dans de nombreuses régions du monde. À l'heure actuelle, la base de données informatisées comprend plus de 75 000 éléments d'information tirés de 627 tentatives d'introduction. Il s'agit d'une source utile pour les participants au projet qui procèdent à l'analyse des facteurs relatifs à la théorie, aux techniques et au succès de la lutte biologique contre les plantes nuisibles.

Introduction

This is a brief report on a collaborative programme that has been titled 'The Silwood International Project on the Biological Control of Weeds'. The main participants in the project are listed in the acknowledgements. The objective of the programme is to elaborate and extend Julien's (1982) database through reference to the relevant literature and, principally, through consultation with acknowledged weed biocontrol practitioners and experts, and to use the new, expanded database for analyses that will improve our understanding of biological control of weeds.

Methods

Julien (1982) lists nearly 600 individual programmes on the biological control of weeds and provides: (i) names and origins of the target weeds; (ii) the names, order, family and origin of each of the agents; (iii) the dates, countries and routes of introduction of the agents; (iv) a brief descriptive evaluation of the success achieved in each case.

These data were used as the starting point in the development of questionnaires designed to gain additional information on the biological characteristics of the introduced insects and mites used for the biological control of terrestrial weeds (Table 1), on the characteristics of the target weeds (Table 2), and on the successes achieved for each attempt at the biological control of weeds (Table 3). The questionnaires, which were circulated to biocontrol practitioners and accepted experts in each field, called for answers to 163 separate questions (some of which were formulated to allow for multiple answers, hence the total of 177 questions on various aspects that are listed in Tables 1–3). Separate questionnaires were completed for each of 627 biological control attempts (questions in Table 1; Table 2, E only; Table 3) and for each of 85 separate terrestrial weed species that have been the target of biological control (questions in Table 2, A–D). All the questions were numerically coded in the questionnaires allowing for input and storage on the University of London Computer and retrieval via a programme package entitled SIR (Scientific Information Retrieval).

Table 1. Number of questions (in brackets) formulated for questionnaires on characteristics of introduced insects and mites used as biological control agents against weeds, world-wide. Separate questionnaires were completed for each attempt with an individual agent species on a specific target weed species, in each country of introduction.

A.	**Identifying the agents** agent order, family, species, origin, target weed species, country of introduction:	(8)
B.	**Characteristics of the agents in their native lands** distribution, abundance, competitors, natural enemies:	(5)
C.	**Biology of the agents** size, feeding habits and guild, reproduction, sex ratio, fecundity, generation time, longevity, diapause, dispersal, host specificity:	(37)

Progress

About 95% of the answers on the questionnaires (in excess of 75 000 pieces of information) have been stored in the computer. The questions that remain to be processed are those listed in Table 2 (A–D) for some weed species. This phase of the project will be complete by the end of 1984 and it will then be necessary to modify and up-date the accumulated information on a regular basis.

Some preliminary analyses have been made using the data and the results are reported elsewhere in these Proceedings (Lawton 1985; Moran and Zimmermann 1985). They indicate the scope and potential for analyses that will improve our understanding of the theory, practice, and success of biological control of weeds.

The data on ratings are to be detailed in a proposed book (edited by V.C. Moran and J.K. Waage) entitled *The Biological Control of Weeds by Introduced Insects: A Practical and Ecological Appraisal,* which will provide accounts on: (i) the data base; (ii) methods for evaluating success; (iii) the population biology of weeds and insect herbivores; (iv) insect–weed interactions; (v) herbivore communities in biological control; (vi) biological control case histories; (vii) analyses of successes and failures; (viii) costs and benefits; and (ix) future prospects for biological control of weeds.

Table 2. Number of questions (in brackets) formulated for questionnaires on weeds that have been targets for biological control using insects and mites. Separate questionnaires were completed for each target weed species.

A.	**Identifying the weeds** family, species, origin, country of introduction, native or introduced, terrestrial or aquatic:	(6)
B.	**Morphology** growth habit, size:	(5)
C.	**Characteristics of the weeds in their native lands** habitat, climate, soil type, water type, distribution, abundance, dominance, taxonomic isolation:	(24)
D.	**Biology of the weeds** generation time, flowering, seed characteristics, asexual reproduction, dispersal, physical and chemical defences, adaptations to fire, allelopathy:	(17)
E.	**Characteristics of the weeds in their countries of introduction** pest status, undesirable and beneficial qualities:	(10)

Table 3. Number of questions (in brackets) formulated for questionnaires on evaluation of success of insects and mites introduced for biological control of weeds, world-wide. Separate questionnaires were completed for each attempt with an individual agent species on a specific target weed species, in each country of introduction.

A.	**Measures of effort (cost)** collection, rearing, screening; 'scientist years':	(9)
B.	**Release data** dates, stages and numbers released, tactics:	(14)
C.	**Success of the agents** impact of agent, area of impact, population growth, time until maximum impact, damage:	(9)
D.	**Effects on target weeds** pest status of weed, distribution, density, and habitats occupied, before and after biological control:	(24)
E.	**Factors limiting success** biotic, abiotic, competition, predators, parasitoids, incompatability with host plant, taxonomic confusion:	(9)

Acknowledgments

The project was initiated during a visit by J.K. Waage to Rhodes University, Grahamstown, from 28 February to 9 April 1982, and owes its inception to the publication by Julien (1982) of his catalogue on the biological control of weeds. The major participants are M.J. Crawley, M.P. Hassell, G. McGavin, V.A. Taylor, and J.K. Waage (Imperial College, University of London, at Silwood Park); M.J. Cock, D.J. Greathead (Commonwealth Institute of Biological Control, at Silwood Park), and D. Schroeder (CIBC, Delemont); P. Harris (Agriculture Canada, Regina); J.H. Lawton (University of York); and V.C. Moran (Rhodes University, Grahamstown). We gratefully acknowledge the generous and sustained support of biological control practitioners in Australia, Canada, the United States of America, Hawaii, Europe, Trinidad, and South Africa.

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The Biological Control of Cactaceae: Success Ratings and the Contribution of Individual Agent Species

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Abstract

Two methods for rating success in the biological control of Cactaceae are compared and discussed. The methods were developed independently, but both lead to the same conclusions: (*a*) the cochineal insects (Dactylopiidae), as a group, have contributed by far the most to the biological control of Cactaceae world-wide; (*b*) *Dactylopius opuntiae* and *D. ceylonicus* have been the most successful biological control agents against cacti, followed by *Cactoblastis cactorum*; (*c*) in relation to the numbers of species imported as potential biological control agents against cacti, and compared to the performance of the dactylopiids and *C. cactorum*, the contribution of the other Hemiptera and Lepidoptera, and of the Coleoptera, Diptera and Acari has been minimal. The implications of these conclusions for the planning and outcome of biological control projects against persistent cactus weeds, such as *Opuntia aurantiaca*, are discussed.

Lutte Biologique Contre les Cactacées: Taux de Succès et Rôle d'Agents Biologiques Particuliers

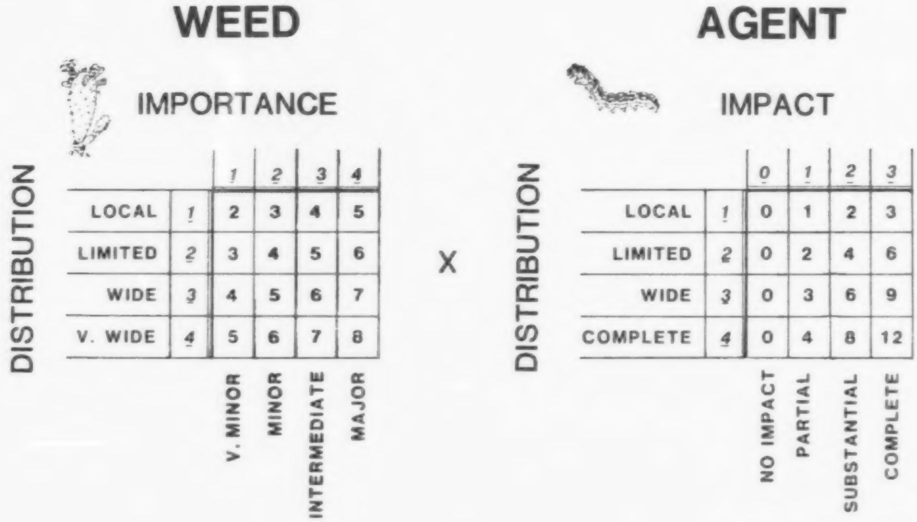
Le rapport compare deux méthodes d'évaluation de l'efficacité de la lutte biologique contre les cactacées. Les deux méthodes ont été conçues séparément; l'une est simple et l'autre plus complexe, mais les deux établissent les mêmes conclusions: (a) *Dactylopius opuntiae* constitue l'agent biologique le plus efficace pour la lutte contre les cactus et *Cactoblastis cactorum* vient au second rang; (b) les cochenilles (Dactylopiidae) constituent le groupe d'insectes de loin le plus efficace dans la lutte biologique contre les cactacées dans le mond entier; (c) en comparaison avec bien des espèces importées comme agents biologiques potentiels pour la lutte contre les cactus et avec l'efficacité des Dactylopiidae et de *C. cactorum*, la contribution des autres hémiptères et lépidoptères et des coléoptères, diptères et acariens a été minimale. Le rapport expose les conséquences que peuvent avoir ces conclusions sur la planification et les réalisations des projets de lutte biologique contre les mauvaises herbes persistantes cactées, comme *Opuntia aurantiaca*.

Introduction

There have been many attempts to evaluate the successes achieved in the biological control of weeds. The simplest of these methods of evaluation have been descriptive accounts in which success is rated as 'partial', 'substantial', or 'complete' (DeBach 1964; Laing and Hamai 1976). More elaborate and informative descriptive evaluations are provided by Goeden (1978) and Julien (1982), in particular. Others have placed emphasis on economic evaluations (Pettey 1950; Simmonds 1967; Huffaker *et al.* 1976; Cullen 1978; Harris and Cranston 1979; Marsden *et al.* 1980). Harris (1979) has measured the costs of biological control in 'scientist years' and later (Harris 1981) discussed methods and purposes of evaluation in general.

What is lacking in these evaluations is a uniformity of method which would allow direct and meaningful comparisons of the successes achieved by different agents on different target weeds in different countries. Apart from the descriptive accounts, there is no way of gaining a perspective in quantitative terms of the contribution of individual agents to the biological control of weeds world-wide.

In this paper we describe two methods that translate subjective descriptions and other evaluations of biological control success into quantitative ratings. The values derived provide estimates of the relative contribution of various agents to the biological control of Cactaceae and also allow some conclusions and predictions that are relevant to past precedents and future strategies in the biological control of cactus weeds.



		1	*2*	*3*	*4*
LOCAL	*1*	2	3	4	5
LIMITED	*2*	3	4	5	6
WIDE	*3*	4	5	6	7
V. WIDE	*4*	5	6	7	8
		V. MINOR	MINOR	INTERMEDIATE	MAJOR

		0	*1*	*2*	*3*
LOCAL	*1*	0	1	2	3
LIMITED	*2*	0	2	4	6
WIDE	*3*	0	3	6	9
COMPLETE	*4*	0	4	8	12
		NO IMPACT	PARTIAL	SUBSTANTIAL	COMPLETE

Fig. 1. Method 1 for rating the success of each biological control attempt for individual species of insects used against specific cactus weeds in different countries. The score for each category is in italics. The scores are additive for the weed, and multiplicative for the agent. The final calculated value for the success rating is the product of the score for the weed and for the agent.

Two Methods for Rating Success

Method 1 was developed by us during preparation of a review on biological control of Cactaceae (Moran and Zimmermann 1985) and the system used is shown in Fig. 1. The distribution and importance of each individual cactus weed species in each country was gleaned from the literature or estimated from personal experience, and scored.

Similarly, the distribution and impact of each individual insect agent, for each biological control attempt in each country was scored. The final value for success rating is the product of the score obtained for the weed and for the agent.

Method 2 was developed independently by Dr. M.J. Crawley and Professor M.P. Hassell (Imperial College, University of London) and is based on questionnaires completed by biological control practitioners as part of the 'Silwood International Project on the Biological Control of Weeds' (Moran 1985). In developing their method, they tried several different means of rating success and included the following criteria in their computer programmes: weed distribution prior to biological control; density of plant cover; area and degree of impact of the biological control agent; perception of the weed as a pest prior to and after biological control; estimates of seven undesirable attributes of the weeds; and estimates of five potentially beneficial attributes of the cactus plants. They also attempted to include values for 'scientist years' (Harris 1979) but data are lacking for most of the programmes analysed. Finally, the following method for rating success produced the most consistent and intuitively satisfactory estimates:

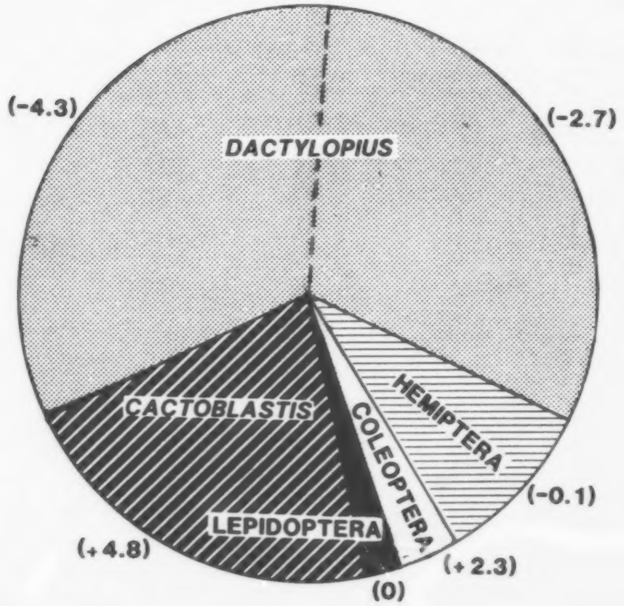


Fig. 2. The relative contribution of various insect taxa to the biological control of cactus weeds, derived from method 2 for estimating success. The percentages in brackets are the differences between the success ratings calculated from method 1 and from method 2.

$$\text{Success rating} = \log w \times d \times a \times (c + 1)$$

where w is the approximate area of weed distribution before biological control (km^2); d is the degree of impact of the agent (no impact is scored as 0, and complete success as 4); a is the area of impact of the agent (no impact is scored as 0, and impact over the complete area of the weed is scored as 4); and c is an estimate of weed cover before biological control (from sparse cover, with a score of 0, to dense cover over the entire distribution of the weed with a score of 2).

Using method 2, success ratings were calculated for all the documented attempts at biological control of Cactaceae world-wide. For some biocontrol programmes, data are lacking and the calculations of success rating were consequently not possible. For both methods, success ratings were calculated for each attempt (introduction) at biological control; i.e. per species of established agent, per target weed species and per country.

Table 1. The success ratings (brackets) of individual insect species as biological control agents against Cactaceae ranked according to: (i) the total contribution of each agent; and (ii) the mean contribution of each species for each attempt at biological control. Only the top seven species of the total of 21 established agents, are listed. For comparative purposes the contribution of *C. cactorum* (asterisk) in the Australian programme against *O. inermis*/*O. stricta*, is given.

Species ranking			
Total contribution		Mean contribution/attempt	
Dactylopius opuntiae (Cockerell)	(844)	**Cactoblastis cactorum*	(155)
D. ceylonicus (Green)	(631)	*Dactylopius ceylonicus*	(105)
Cactoblastis cactorum (Berg)	(507)	*D. opuntiae*	(53)
		D. austrinus	(48)
Chelinidea tabulata (Burmeister)	(118)	*Hypogeococcus festerianus*	(44)
D. austrinus De Lotto	(97)	*D. tomentosus*	(36)
Hypogeococcus festerianus (Lizer y Trelles)	(87)	*Cactoblastis cactorum*	(27)
D. tomentosus (Lamark)	(72)	*Chelinidea tabulata*	(20)

Success Ratings by Taxon

When the results from the two methods were compared (Fig. 2) they were remarkably similar in estimating the contribution to biological control of various agents, arranged by taxon. The two methods also produced the same ranking sequence for the most important species involved (Table 1). Because of the extensive data base that has been accumulated during the 'Silwood Project' and because values for success ratings are more easily generated by computer, method 2 was used exclusively in the following account.

Fig. 3 shows the mean success ratings for five taxa of cactophagous insects that have been used in the biological control of Cactaceae world-wide. The mean success ratings were calculated for each *established* species for all of the biological attempts against cactus weeds.

Fig. 3 illustrates the dominance of the dactylopiids as biological control agents against Cactaceae. Mean success ratings for Lepidoptera, including *Cactoblastis cactorum* (Berg) (Pyralidae), are less impressive than for dactylopiids. Most of the recorded contribution to biological control for Lepidoptera is by *C. cactorum* on *Opuntia inermis* (DC.) DC. and *O. stricta* (Haworth) Haworth in Australia. The contribution of the other Hemiptera which includes two *Chelinidea* spp. (Coreidae) and *Hypogeococcus festerianus* (Lizer & Trelles) (Pseudococcidae) is relatively modest; the contribution of the Coleoptera is poor, and the Diptera failed completely. These measures of success confirm the relative contributions shown in Fig. 2.

In relation to the number of species of cactophagous insects introduced for the biological control of cactus weeds world-wide (inset to Fig. 3), the rates of establishment and successes achieved have been particularly poor for the Coleoptera and Lepidoptera (apart from *C. cactorum*) and, by contrast, outstanding for the dactylopiids.

Success Ratings for Individual Species

The total contribution of individual agents to the biological control of Cactaceae, derived from the calculated success ratings, are shown in Table 1. *Dactylopius opuntiae* (Cockerell) and *D. ceylonicus* (Green) (Hemiptera: Dactylopiidae) have made the greatest contribution to biological control followed by *C. cactorum* (which is the only non-hemipteran in the seven top-ranked species).

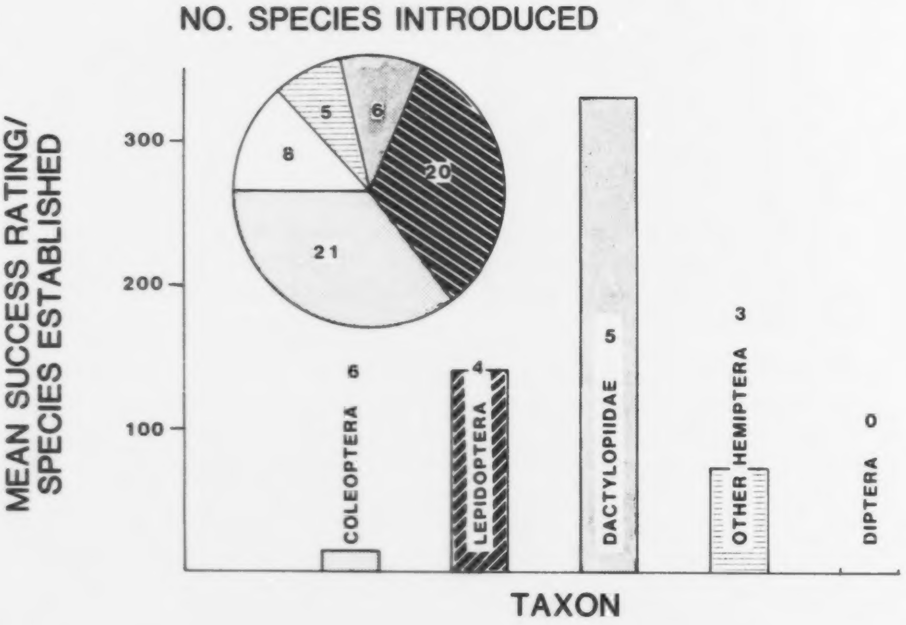


Fig. 3. The mean success rating for each established species of insect in the biological control of Cactaceae. Above each histogram bar are the numbers of species established for each taxon. The pie-diagram shows the total number of insect species introduced for the biological control of cactus weeds, arranged by taxon.

On the basis of the mean contribution of the individual species per attempt (Table 1), the three *Dactylopius* species (*D. ceylonicus*, *D. opuntiae*, and *D. austrinus* De Lotto) are ranked highest, followed by *H. festerianus*, *D. tomentosus* (Lamark), *C. cactorum*, and *Chelinidea tabulata* (Burmeister). Again, the rating for *C. cactorum* in the case of the biological control campaign against *O. inermis/O. stricta* in Australia is high (155) in comparison to the other ranked species, and much higher than the mean rating (27) for all the attempts using *C. cactorum* world-wide.

Discussion

This paper describes two rating systems that estimate the success of the biological control agents which have been used against Cactaceae on a world-wide basis. The two methods produced quantitative values from partly subjective estimates of the successes achieved, and both methods gave remarkably similar results.

The success ratings have produced the following perspectives and insights: (i) the success ratings have allowed a comparison of the relative contributions of all the insect agents involved in the biological control of cactus weeds; (ii) this has highlighted the outstanding contribution of the dactylopiids, particularly *D. opuntiae* and *D. ceylonicus*, and this conclusion is consistent whether the success ratings were totalled, or calculated as mean values per attempt, or per species established; (iii) the success ratings have emphasised the distorted view gained by biological control practitioners and others, which is perpetuated in the literature, about the dominant role of *C. cactorum* as a biological control agent against cacti. We have shown that, apart from the much publicised and spectacular achievements of *C. cactorum* on *O. inermis/O. stricta* in Australia, and in some other countries on a smaller scale, the contribution of *C. cactorum* has been over-rated and certainly overshadowed by that of the dactylopiids; (iv) the success ratings have emphasised the poor performance of all other Lepidoptera apart from *C. cactorum*. There seems to be no obvious reason why other Lepidoptera, including at least four other species of *Cactoblastis* that have been introduced for biological control of cacti, and which have similar biological characteristics, including the production of egg-sticks and gregarious larvae, have not resulted in similar successes to those achieved by *C. cactorum*; and (v) the success ratings have also emphasised the relatively poor contribution of the Coleoptera in the biological of cactus weeds.

These success ratings are of consequence in directing future strategies for the biological control of cactus weeds that remain as chronic problem plants, such as *O. aurantiaca* Lindley in South Africa. Firstly, the precedent with *C. cactorum* as a biological control agent has led to repeated attempts to establish other Lepidoptera species, and this now appears to be a poor strategy; the success ratings also suggest that no emphasis should be placed on exploration for cactophagous Coleoptera or Diptera. Secondly, because there seems to be little chance of finding new dactylopiid species in the Americas, the emphasis in the biological control of cacti should shift to the use of pathogens in combination with plant-sucking bugs that are known to act as mechanical transmitters of fungi that destroy cactus tissue.

Lastly, attempts to rate the success of biological control agents used against Cactaceae, and other weeds such as *Lantana* (Verbenaceae), which has been part of the 'Silwood Project', have emphasised the importance of detailed documentation in the evaluation of biological control programmes. Adequate pre- and post-release studies and detailed records of results will be the cornerstone of future efforts to improve the assessment of biological control and to relate these assessments to economic values. Cullen (1978) and Harris (1981) have previously stressed the need for detailed documentation in the evaluation of biological control programmes, and one of the objectives of the 'Silwood Project' is to provide a uniform data base of information which may be used by biological control practitioners to develop improved methods for the evaluation of the biological control of weeds.

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How Many Insect Species are Necessary for Successful Biocontrol of Weeds?

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Abstract

The conventional wisdom of classical biological weed control is that as more insects are established on weeds the damage to the plants increases and the goal of successful biological control is gradually approached. I test this hypothesis by comparing the reduction in seed production of knapweed achieved by several insects attacking the same plants, and by reviewing reported successes in the biological control of weeds. Observations don't support a model of cumulative insect attack leading to biological control. Multiple attack by different insect species introduced on knapweed in British Columbia varied from being slightly advantageous, to having little influence, to being slightly deleterious, as compared to attack by a single species. A review of 26 successful weed control programs shows that in 81%, success was achieved by a single insect species. These observations suggest that biological weed control is more frequently achieved by a single insect species rather than the cumulative effect of several insect species. I suggest that each insect introduction is a lottery and may lead to successful biological control.

Combien d'Espèces d'Insectes Sont-elles Nécessaires à la Lutte Biologique Efficace Contre les Plantes Nuisibles?

L'introduction de 107 espèces d'insectes a permis d'assurer une lutte biologique efficace contre 26 espèces de plantes nuisibles (moyenne de 4,1 introductions par plante nuisible). Parmi les populatoins d'insectes introduites, 74 (70%) se sont établies. L'efficacité de la lutte a été attributée à une espèce d'insecte dans 16 cas (62%), deux insectes dans 5 cas et 3 insectes dans un cas. Dans trois des cinq cas où une lutte efficace a été assurée par deux espèces d'insectes et dans l'unique cas où l'efficacité de la lutte a été attributée à trois espèces d'insectes, les agents biologiques étaient *Cactoblastis cactorum* et *Dactylopius opuntiae* et les plantes hôtes, des cactus. Aucun des cas où le succès de la lutte a été attribué à plus d'un insecte n'a été suffisamment documenté. Le succès des méthodes repose sans doute davantage sur le hasard, car l'introduction de l'espèce d'insecte la plus appropriée au site donne de meilleurs résultats que l'essai cumulé d'un certain nombre d'insectes moins adaptés. Il est difficile d'identifier les espèces d'insectes les plus propices à la lutte biologique. Des insectes étroitement apparentés, présentant des phénologies et des comportements d'infestation similaires, n'ont pas nécessairement le même succès comme agents biologiques. L'étude donne comme exemple *Chrysolina quadrigemina* et *C. hyperici*, deux insectes étroitement apparentés, mais dont l'un est efficace, l'autre non.

Introduction

The aim of biological weed control is to decrease the population of weeds through the establishment of insect herbivores or plant diseases. Harris (1979) reports that an average of four species were established in successful biological control projects. This could be interpreted to indicate that the cumulative stress of several herbivore species was frequently required before control was achieved (Harris 1985). On the other hand, successful biological control is the exception and has been achieved in only approximately 30% of the attempted programs. This lack of success suggests that many insects have little effect on the population density of plants or that many plants are able to compensate for herbivore damage (for recent examples see Hendrix 1984; Islam and Crawley 1983; McNaughton 1983; Solomon 1983).

To test the generality of the conventional wisdom that more insect herbivory is better for weed control, I report observations of the seed reduction achieved in diffuse (*Centaurea diffusa* Lam.) (Compositae) and spotted (*C. maculosa* Lam.) knapweed by several introduced insects. In addition, information from Julien's (1982) review, 'Biological Control of Weeds' is summarized to determine the number of insect species involved in successful weed control projects.

Methods

The number of *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae) and *Urophora quadrifasciata* (Mg.) (Diptera: Tephritidae) in seed heads of spotted knapweed was scored in the late summer of 1979 and 1980 in plants collected from the release site near Westwold, B.C. The number of seeds in heads with no insects, one insect species, or both species was counted.

Table 1. Mean number (SD) of *Urophora* and *Metzneria* in heads attacked and not attacked by the other species.

		Metzneria			
		Present		Absent	
	1978	0.51	(0.94)	0.24	(0.63)
Urophora/head	1979	0.89	(0.93)	1.00	(1.39)
	1980	1.18	(1.64)	1.06	(1.89)
		Urophora			
		Present		Absent	
	1978	0.37	(0.44)	0.38	(0.45)
Metzneria/head	1979	0.65	(0.52)	0.56	(0.54)
	1980	0.70	(0.49)	0.48	(0.50)

To study the interactions between *Urophora* and a root-boring beetle, seed production of diffuse knapweed was assessed by counting the proportion of buds which developed to form seed heads in diffuse knapweed plants from the White Lake area south of Penticton, B.C. in 1981. *Urophora* attack was scored by counting the number of galls in five distal heads on each plant and plants were scored as to whether they were attacked by *Sphenoptera jugoslavica* Obenb. (Coleoptera: Buprestidae).

Results

Multiple Introductions on Knapweed

Six insects have now been introduced on knapweed, *C. diffusa* and *C. maculosa*, in British Columbia (Harris and Myers 1984). We have attempted to measure the interactions between pairs of these agents to determine if in general they are complimentary. Two species of gall-flies, *Urophora affinis* Frauenfeld and *U. quadrifasciata* have been introduced to B.C. Although the mean number of each species was lower in flower heads containing larvae of both flies, the total fly density was approximately 35% higher on average in the heads attacked by both species. We don't have enough information on well-established populations of one *Urophora* species to compare to populations with both fly species. In Europe the density of flies in areas where both species were present tended to be lower than in areas inhabited by only one species (Myers and Harris 1980). Therefore where several insect species have evolved together, interactions among species can reduce their combined impact on plants. This negative interaction has not yet been observed in B.C.

The seed feeding moth, *M. paucipunctella* has previously been reported to kill co-occurring larvae of *Urophora* (Englert 1971; Varley 1947). We found no evidence of a reduction of *U. quadrifasciata* in seed heads of spotted knapweed containing both insect species (Table 1). In Westwold, B.C., *Urophora* reduced seed production of spotted knapweed by 28–35% in the two years studied when they occurred in seed heads by themselves (Table 2). The percent seed reduction in heads with both *Urophora* and *Metzneria* was 20–41% in those same years. We calculated that *Metzneria* larvae eat approximately three to four seeds for larval development; this is approximately 20–30% of the average number of seeds/head.

Table 2. Mean number of seeds/flower head (SE) of spotted knapweed heads attacked and unattacked by *Urophora* and *Metzneria* in 1979 and 1980 at Westwold, B.C. Percent reduction in seed production is based on number of seeds in heads unattacked by either species.

	Metzneria			
	Present		Absent	
Urophora	1979	1980	1979	1980
Present	12.6 (0.6) −20%	9.9 (0.6) −40%	10.3 (0.8) −35%	12.1 (0.9) −28%
Absent	18.5 (0.8) +17%	13.4 (0.7) −20%	15.8 (0.8) Control	16.8 (0.6) Control

Harris (1980) records that *Urophora* densities of 1.9/spotted knapweed flower head reduced seed production by 67%. In 1980 the mean density of *Urophora* at the Westwold site was a little over 1/head and the density of *Metzneria* approximately 0.5/head. The combined reduction in seed numbers in attacked heads was approximately 40%, which is slightly below the total seed reduction in an area with a well-established *Urophora* population. These data indicate that two insects aren't greatly better than one.

At the White Lake area near Penticton three introduced insect species are now established on diffuse knapweed, *U. affinis*, *U. quadrifasciata*, and *S. jugoslavica*. In September 1981, samples of plants were collected to determine the level of attack of *Urophora* and *Sphenoptera*. Generally only one *Sphenoptera* larva develops in the root of the plant and previously-attacked plants can easily be identified from the damage. *Urophora* attack was determined by sampling five distal seed heads on the plants. The level of attack by *U. affinis* was the same in plants attacked by *Sphenoptera* and unattacked plants (Table 3). However, attack by *U. quadrifasciata* was significantly lower on plants attacked by *Sphenoptera*.

The density of *Urophora* at this site was 1.63 larvae/head (*SE* = 0.30) based on a count of all the seed heads of 23 plants. This is high as compared to previously sampled populations of *Urophora* on diffuse knapweed in B.C. and considerably higher than European densities (Myers and Harris 1980). The influence of insect attack was assessed by the proportion of total buds which developed to produce seed heads. In 1981 the actual number of developed heads was not reduced on plants attacked by *Sphenoptera*, 45.5 ($SE = 4.9$) for attacked plants and 35.1 ($SE = 3.9$) for unattacked plants, and the proportion of heads developed on attacked and unattacked plants was the same (Table 3). However when *Urophora* attack was considered, the proportion of seed heads which developed on plants attacked by *Sphenoptera* was actually greater for plants with a high level of *Urophora* attack (> 10 larvae in 5 distal heads) than in plants with a low level of *Urophora* attack (Table 4). This was not the case for plants unattacked by *Sphenoptera*.

Number of Agents in Successful Control Programs

In Julien's (1982) review, 26 weed species were recorded as having been successfully controlled. The average number of insect species introduced in each of these successful projects was 4.1 and the success rate of establishment was approximately 70% (2.8 insect species/plant). Eighty-one percent of the successes were attributed to a single species. In four cases success was attributed to two insect species, with *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) and *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae) being involved in two of these examples. A single case in which success was attributed to three insect species also involved the control of cactus with *Cactoblastis* and *Dactylopius*, but a cerambycid beetle was also thought to have contributed to control.

Table 3. Mean number of *Urophora* larvae (SE) in five distal seed heads of diffuse knapweed plants attacked by *Sphenoptera* and unattacked plants.

	Sphenoptera	
Urophora sp.	Attack	No Attack
U. affinis	9.9 (1.2)	9.3 (1.3)
U. quadrifasciata	0.9 (0.4)[1]	2.8 (0.8)[1]

[1] Means significantly different with a T-test ($P<0.05$).

Discussion

I conclude from the study of knapweed that the influence of several insect species attacking plants in the same vicinity varies from being slightly complimentary (two *Urophora* species) to making little difference (*Urophora* and *Metzneria*) to possibly being slightly deleterious (*Urophora* and *Sphenoptera*). The ability of plants to compensate for insect damage contradicts the assumptions of a simple cumulative model for insect attack. A little insect attack may stimulate plants rather than stress them. Knapweed cannot be considered to be successfully controlled in British Columbia at this time, even in sites where several insect species are well established.

The history of biological weed control indicates that a single species of insect most frequently is sufficient for successful control. This would indicate that only some insects are capable of reducing the density of their food plants. The challenge is to identify these species for introduction.

If biological control successes are achieved by the chance introduction of an effective species in the appropriate location, we might think of success in terms of a lottery model rather than a cumulative stress model as proposed by Harris (1985). With every introduction comes the possibility of success. Once the successful agent becomes established it will largely displace the other agents. Different agents may be successful in different environments, and successful control may only be achieved in certain environments.

It remains a question if successful agents can be selected in a manner to change the odds in the lottery. The example of *Chrysolina hyperici* (Forster) and *C. quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) shows that two very closely related insect species can vary in their ability to control *Hypericum* (Clusiaceae) even though they are very similar in their life cycles and the damage they do to plants (Williams, Myers and Edwards, unpubl. data). The important difference seems to be that the environment which selects for a preponderance of *C. hyperici* also is conducive to *Hypericum* seedling establishment. The reproductive pattern of the plant is the factor which determines the success of the biological control agent, not the characteristics of the agent itself.

Successful biological control programs show that insects can control the density of their food plants. The experimental removal of insect herbivores from native weed populations may be very helpful in identifying plants with potential for successful biological control.

It may be of little importance to the mechanics of biological control whether the cumulative stress or lottery model pertains. But preconceived notions can influence how data are collected and interpreted. We should avoid the assumption that all established species contribute to the control of a particular weed.

Table 4. Mean proportion (SE) of seed heads developed on plants attacked by *Sphenoptera* and unattacked plants with high and low *Urophora* attack.

Mean *Urophora*/head	Attacked by *Sphenoptera*	Unattacked
<10	0.38 (0.03)[1]	0.42 (0.07)
>10	0.51 (0.04)[1]	0.47 (0.05)

[1] Values significantly different from each other ($P < .05$, T-test).

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Egg Predation by Ants as a Partial Explanation of the Difference in Performance of *Cactoblastis cactorum* on Cactus Weeds in South Africa and Australia

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Abstract

The mediocre performance of *Cactoblastis cactorum* in controlling *Opuntia ficus-indica* and *O. aurantiaca* in South Africa has been attributed mainly to incompatibility with these host plants. Mortality is high during larval penetration of the plants and larvae are unable to destroy woody cladodes. Life tables derived from a study of *C. cactorum* at a site near Grahamstown demonstrate the important role of egg predation by ants in reducing the effectiveness of *C. cactorum*. The consequence of this predation pre-empting density-dependent mortality in the larval stage is discussed. Available evidence suggests that egg predation is not as high in Australia as in South Africa. The greater impact of ants in South Africa partly explains the difference in performance of *C. cactorum* compared with that in Australia.

La Prédation des Oeufs par les Fourmis Explique, en Partie, les Différences Observées dans la Performance de *Cactoblastis cactorum* Comme Agent Biologique Contre les Plantes Nuisibles Cactées en Afrique du Sud et en Australie

La performance médiocre de *Cactoblastis cactorum* dans la lutte contre *Opuntia ficus-indica* et *O. aurantiaca* en Afrique du Sud a été attribuée principalement à l'incompatibilité qui existe entre l'insecte et ces plantes hôtes. Le taux de mortalité est élevé pendant la pénétration des larves dans les plantes, et les larves sont généralement incapables de détruire les cladodes ligneux. Les tables de survie tirées d'une étude sur *C. cactorum* en un site près de Grahamstown montrent que la prédation des oeufs par les fourmis réduisent considérablement l'efficacité de *C. cactorum*. L'auteur traite des répercussions de la prédation qui remplace les causes de mortalité liées à la densité au cours de l'étape larvaire. Les espèces de fourmis qui infestent *C. cactorum* sont plus nombreuses en Afrique du Sud qu'en Australie, tandis que la diversité des autres ennemis naturels est similaire dans les deux pays. La prédation par les fourmis, qui est plus important en Afrique du Sud, explique, dans une certain mesure, les différences dans l'efficacité de *C. cactorum* constatées dans les deux pays.

Introduction

The spectacular success in Australia of *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) in controlling the shrub pears, *Opuntia inermis* (DC.) (Cactaceae) and *O. stricta* (Haworth) Haworth, was not repeated when it was introduced to South Africa against the tree pear, *O. ficus-indica* (L.) Miller. This has been attributed to *O. ficus-indica* being more resistant to attack because it has a high proportion of woody cladodes, which *C. cactorum* larvae are usually unable to destroy (Pettey 1948; Monro 1975; Annecke and Moran 1978). *C. cactorum* also feeds on the narrow-jointed pear *O. aurantiaca* Lindley which is a weed in South Africa and Australia. The woody basal cladodes of this species are also resistant to *C. cactorum* attack and larvae rarely kill entire plants (Dodd 1940; Pettey 1948; Moran and Annecke 1979). Woody cladodes not only prevent the complete destruction of *O. ficus-indica* and *O. aurantiaca* plants but also reduce the survival of larvae feeding in them (Pettey 1948).

The results presented below are based on a study at one site in South Africa in which oviposition, detailed life tables and effectiveness of *C. cactorum* as a biological control agent were compared for *C. cactorum* populations on *O. ficus-indica* and *O. aurantiaca*. Factors other than host plant resistance have reduced population levels of *C. cactorum* at this site, and one of the most important of these was predation of eggs by ants. The role of egg predation by ants in reducing the effectiveness of *C. cactorum* is discussed and compared in South Africa and Australia from these results and from published records.

Table 1. Comparison of mortality and fecundity of *Cactoblastis cactorum* (Berg) in South Africa on *Opuntia ficus-indica* (L.) Miller and in Australia on *O. inermis* DC.

	South Africa on *O. ficus-indica*		Australia on *O. inermis*
Parameter	This study	Pettey (1948)	Dodd (1940)
% egg mortality	74	—	—
% penetration mortality[1]	19	—	16
% total larval mortality	54	—	40–60
% pupal parasitism	5	16	13
% other pupal mortality	35	35	25
% adult mortality — summer	46	—	—
% adult mortality — winter	84	—	—
Mean fecundity/female	(175)[2]	126	136

[1] Only includes mortality of whole colonies and not mortality within colonies.

[2] This value is higher than the other two because it does not include females that did not lay eggs, and was determined from tests undertaken in the laboratory, under optimal temperature conditions.

Methods

All field work was undertaken on a farm 19 km NW of Grahamstown. Seven adjacent 50 × 50 m quadrats were marked and all *O. ficus-indica* plants ($n = 194$) and *O. aurantiaca* clumps ($n = 1316$) contained in the quadrats were individually numbered. *O. aurantiaca* clumps consist of a cluster of intermingled plants of different sizes which for convenience are referred to as plants. To determine egg mortality, all *O. ficus-indica* plants and a sample of *O. aurantiaca* plants were searched almost daily for eggsticks during the summer (October to December) and winter (February to May) egg-laying periods. Each eggstick was numbered, the number of eggs was counted, and egg mortality was checked on each subsequent day.

Results and Discussion

A comparison of penetration mortality, total larval mortality, and fecundity, which are all host plant-related factors, suggests that in *C. cactorum*, they are similar on *O. ficus-indica* in South Africa and *O. inermis* in Australia (Table 1): (1) penetration mortality was only 2–3% higher on *O. ficus-indica*; (2) total larval mortality on *O. ficus-indica* was within the range of 40–60% cited by Dodd (1940) for *O. inermis*;

and (3) average fecundity/female, based on Pettey's (1948) and Dodd's (1940) figures, was 7% lower on *O. ficus-indica*.

The reason why the greater host plant resistance of *O. ficus-indica* is not markedly reflected in these results is because, firstly, females oviposit mostly on terminal, succulent cladodes (Robertson, unpubl. data) and secondly, succulent cladodes are usually sufficient for the food requirements of larvae. Except on small plants, larvae on plants at the study site were rarely at densities where they were forced to feed on the woody cladodes.

Drawing conclusions from the above results has risks as parameters were measured and data were interpreted in different ways. However, the data indicates that difference in performance of *C. cactorum* in South Africa and Australia cannot be entirely linked to differences in the resistance of the two host plants to attack. Table 1 shows that other factors might also be responsible. Dodd (1940) does not give values for egg mortality of *C. cactorum* in Australia but results in Table 1 show that in the study area in South Africa it was very high. Pupal parasitism, based on the extensive results of Pettey (1948) and Dodd (1940), is only about 3% higher in South Africa, but mortality of pupae from other factors is 10% higher than in Australia. Adult female mortality (= pre-oviposition egg mortality) has not been measured in Australia, but in South Africa was deduced indirectly in this study as 46% in the summer 1981–82, and 84% in the winter 1982 generation. Low temperatures reduce fecundity and decrease survival of females (Pettey 1948) which probably accounts for the high mortality in the winter generation. In Australia, temperature also affects fecundity and adult mortality (Dodd 1940), but whether it does so to the same extent as in South Africa is not known.

The high mortality of *C. cactorum* eggs recorded in this study is mostly due to predation by at least eight species of ants. Recorded species are: *Crematogaster liengmei* Forel, *Pheidole* sp., *Tetramorium erectum* Emery, *T. bacchus* Forel, *Tetramorium* sp., *Monomorium albopilosum* Emery, *M. minutum* Mayr., and *Camponotus niveosetosus* Mayr. An unidentified mite and a lygaeid bug (*Nysius* sp.; Hemiptera: Lygaeidae) were also recorded as predators of *C. cactorum* eggs, but in relation to ants their effect is of minor importance. In addition to egg predation, eggsticks were sometimes broken off, either partly or completely, by adjacent vegetation brushing against them or by hail, heavy rain and wind.

There are four main reasons why egg predation by ants has been an important mortality factor affecting the *C. cactorum* population in this study: (1) *Magnitude*. Egg predation, mainly by ants, caused 60 and 55% mortality of eggs laid on *O. ficus-indica* in the summer 1981–82 and winter 1982 generations, respectively. These values were considerably higher on *O. aurantiaca*, accounting for 77 and 78% mortality respectively in each generation (Fig. 1). Observations in four other generations at the same site confirm that high egg predation is a general phenomenon. (2) *Life stage attacked*. Predation before the larval stage can decrease the amount of weed destruction more than the same amount of predation after this stage, as predation directly affects the proportion of eggs laid that hatch. The importance of this factor depends on the extent of density-dependent larval mortality, but this was not great in this study. (3) *Density-dependence*. There is evidence that predation by ants of *C. cactorum* eggs is spatially density-dependent (Robertson, unpubl. data). This factor could increase the dampening of *C. cactorum* populations caused by egg predation, although other factors such as season and prevailing temperatures tend to obscure its effects. (4) *Ants are generalists*. *C. cactorum* eggs would form only a small fraction of the food consumed by each of the ant species that feed on them. Eggstick density would therefore have little effect on ant population numbers and ants would respond directly to changes in eggstick densities between generations. In addition, ants are attracted onto *O. ficus-indica* and *O. aurantiaca* plants by extra-floral nectar production and this might further increase the speed of their response to eggstick presence.

Predation of *C. cactorum* eggs by ants appears to be widespread in South Africa, although in some areas other factors might be more important in limiting population numbers. I have observed extensive egg predation in a valley-bushveld site near Uitenhage and in Fish River scrub vegetation near Fort Brown. Pettey (1948) found that ants attacked all stages of *C. cactorum* except the adult and considered that they had probably caused more mortality of *C. cactorum* in South Africa than any other predators. He recorded that several species of small ants removed eggsticks from the paper quills in which they had been placed for distribution purposes. He reports on an experiment in which predation of eggsticks in paper quills was measured at seven sites. At five of these sites, only 2–7% of the eggsticks were removed from the quills, whereas at the other two sites ants caused 30 and 59% mortality. These results are under-estimates for two main reasons. Firstly, eggsticks of unknown age were used. Thus, during the experiment, eggsticks were not exposed to predation for their entire development period. Secondly, these tests were conducted in May (winter). Ant

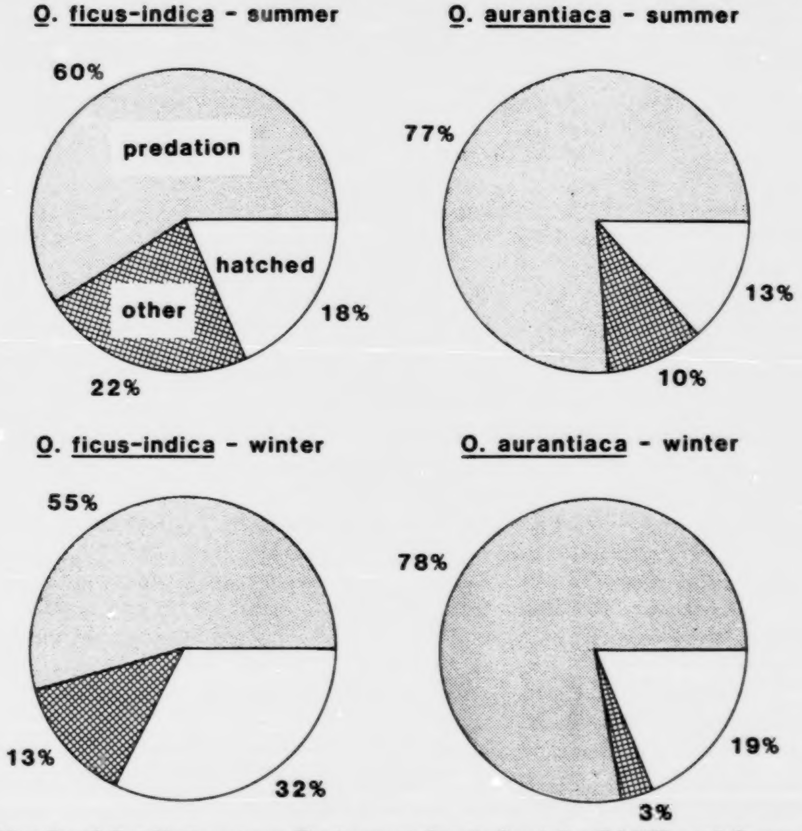

Fig. 1. Mortality of *Cactoblastis cactorum* (Berg) eggs on *Opuntia ficus-indica* (L.) Miller and *O. aurantiaca* Lindley in the summer 1981–82 and winter 1982 generations at a site near Grahamstown.

predation of eggs is strongly influenced by season and prevailing temperatures (Robertson, unpubl. data). For instance, at the study site near Grahamstown, predation was at its peak during March, dropped sharply during April, and by May was at a low level. Of the eggs remaining on *O. ficus-indica* plants at the beginning of May, only 16% were eventually destroyed by ants.

Ant predation of *C. cactorum* eggs also occurs in Australia, but available evidence suggests that it is not as severe as in South Africa. Dodd (1940) records egg predation by *Iridomyrmex* ants but regarded this as being unusual. He mentions that small ant species, such as *Crematogaster*, may eat some of the eggs in a stick but does not detail the extent of this predation. Compared with Australia, there are more ant species recorded attacking *C. cactorum* in all its stages in South Africa while the diversity of other natural enemies is similar.

During a study of eggstick clumping on *O. inermis* in Australia, Monro (1967) located 1178 eggsticks at eight different sites, but makes no mention of egg predation affecting his estimates of eggstick densities. Later (Monro 1975), he mentions that in the southern part of the range of *C. cactorum* in Australia, there is 'an almost classic two species interaction with little interference from predators or competitors'. White (1981) determined eggstick densities on *O. inermis* plants, but also does not mention egg predation. In the study undertaken near Grahamstown, 49% of eggsticks on *O. ficus-indica* were completely destroyed by ants at the end of the summer and winter generations, many of which had completely disappeared. Eggstick densities would therefore have been very under-estimated if the same methods as Monro (1967) and White (1981) had been used.

Hoffmann (1981) recorded 80% mortality of *Tucumania tapiacola* Dyar (Lepidoptera: Pyralidae) eggs in South Africa caused mostly by ants. The reason this moth was successfully established on *O. aurantiaca* in Australia (Dodd 1940) but not South Africa (Hoffmann 1982) is possibly related to the excessive egg predation by ants occurring in South Africa.

There is a need for clarification on the extent of predation by ants of *C. cactorum* eggs in Australia. Available evidence, however, suggests that whereas in Australia, population numbers of *C. cactorum* are limited by density-dependent larval mortality, in South Africa, larval densities are often kept at low levels by other mortality factors — especially ant predation in the egg stage. Even if population levels of *C. cactorum* were much higher, its performance on *O. ficus-indica* and *O. aurantiaca* would still not match that on *O. inermis* and *O. stricta* in Australia because it is inefficient at destroying woody cladodes. Nevertheless, *C. cactorum* can destroy *O. ficus-indica* plants with less than 15 cladodes (Zimmermann and Malan 1981) and also reduces the size and vigour of *O. aurantiaca* and large *O. ficus-indica* plants. Egg predation has lowered the extent of this damage.

Acknowledgments

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Plant Architecture and How Biological Control Agents Affect the Dynamics of Weeds

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Abstract

Plants are constructed of modules such as roots, shoots and leaves, which are produced in a genetically determined pattern or architecture. Plants respond to the environment more by changing the number and distribution of these modules rather than the size of modules. The importance of damage by biological control agents for plant dynamics depends not only on the amount of tissue destroyed but also on the age and position of the modules damaged. Age and position determine the importance of a module to a plant and to its potential to grow and reproduce. It is suggested that the relative effectiveness of different control agents might be better understood by comparing their effects on plant architecture. Use of this architectural approach is illustrated for insects attacking the floating weed *Salvinia molesta*.

Configuration des Plantes et Effets des Agents de Lutte Biologique sur la Dynamique des Plantes Nuisibles

Les plantes sont constituées de modules, comme les racines, les pousses et les feuilles, qui se développent selon un modèle ou une configuration génétique déterminée. Elles réagissent davantage à leur milieu par la modification du nombre et de la distribution de leurs modules plutôt que par la modification de la taille des modules. Sur le plan de la dynamique des plantes, l'importance des dégâts dépend non seulement de la quantité de tissus détruits mais également de l'âge et de la position des modules endommagés. L'âge et la position déterminent dans quelle mesure un module est important pour le plant entier actuel et pour le potentiel de croissance et de reproduction de ce dernier. Des insectes qui attaquent la plant nuisible flottante *Salvinia molesta* sont utilisés pour illustrer comment l'étude de la configuration des plantes peut permettre de comprendre le rôle des agents biologiques.

Introduction

Though plants stay still to be counted, there are difficulties in studying their population dynamics which are not usually encountered in studies of animals. Levin (1976), for example, discussed the difficulty of defining a species when there is such a range of breeding systems among plants and Harper (1977), White (1979) and Whitham and Slobodchikoff (1981) discussed the difficulty of defining an individual when there is such a range of cloning and somatic mutation among plants. Harper (1976) made the distinction, followed here, between genets, or genetic individuals each derived from a single zygote, and ramets, or ecological individuals which can live independently even though a number may have originated from a single zygote. His restriction of the term reproduction to the production of new zygotes (Harper 1977) is also followed.

Ramets are themselves composed of populations of parts, or modules, such as leaves, shoots and branches. Ramets usually respond to their environment more by changing the number and arrangement of the modules they produce rather than changing the size or shape of individual modules (Bradshaw 1965; Harper 1977). Plants depend on diffuse resources and, unlike all animals except colonial ones such as hydroids, growth generally results in increased capture of resources as well as increased costs of maintenance. Most plants respond to shortages by shifting investment into growth of those parts which capture whatever resource is limiting. Shoot–root ratios, for example, can vary enormously depending on whether light or water and nutrients are in short supply. At any moment, particular modules of a plant are sources and other are sinks for particular resources. The source/sink role depends not only on type of module, but changes with a module's age and position within a plant. The effects of damage therefore depend on ages and positions of modules damaged as well as on their types.

Most herbivores and plant pathogens attack certain kinds of modules and not others, for example leaves but not roots or stems, and they usually prefer only those modules of particular ages in particular positions on the plant because of variations in toughness, nutrient content, defensive chemicals or microclimate (Denno and McClure 1983). This paper describes a way of relating attack on specific modules to growth of ramets and the dynamics of populations of ramets.

The Concept of Plant Architecture

Though it is unusual for two ramets to have an identical arrangement of modules, it is common experience that structural variation is within limits which allow fairly accurate identification of ramets to species based on general shape alone. Halle *et al.* (1978) have extended this observation into the concept of a genetically encoded 'architectural model', or arrangement of modules, which is expressed most fully under conditions optimal for growth. The architecture is expressed through genetic control of the angles and sequence of branching, and of whether indeterminate vegetative or determinate reproductive modules will be produced. Growth hormones and electrical and pressure gradients control when meristems will divide, the sequence in which the resultant parts will grow or remain dormant, and the types of modules produced (Leopold and Kriedemann 1975).

Under sub-optimal conditions the architectural model is expressed less completely, with the details of expression depending on the exact position and timing of environmental factors. For example, shading on one side of a tree commonly reduces the production of branches on that side. Ward (1964), Gill (1971), Fisher and Tomlinson (1973) and Maillette (1982*a*, *b*) have shown that the expression of architecture by a plant can be defined by the probabilities that meristems will develop into modules of particular types within certain intervals of time.

Architecture and Plant Population Dynamics

The architecture of a plant imposes constraints on the rate of increase of populations of each type of module, and in this way on the growth of individual ramets. For example, a plant which branches by apical bifurcation has the potential for much faster growth than a plant which produces lateral branches (Fig. 1). Through growth of individual ramets, the architecture imposes constraints on increase of populations of ramets (and genets) because faster-growing ramets become larger and can produce more offspring, whether by reproduction or vegetative proliferation.

Similarly, sexual reproduction requires that some meristems develop into reproductive modules, leaving fewer meristems to continue indeterminate growth. This reduces the size of a ramet, the number of reproductive modules and the number of vegetative propagules which can be produced later. Watson (1984), for example, found that vegetative production of new ramets in flowering compared with non-flowering clones of water hyacinth (*Eichhornia crassipes* [Mart.] Solms-Laubach; Pontederiaceae) was limited by the availability of meristems rather than availability of resources.

In environments varying in time, there will be a tradeoff between committing meristems to reproductive modules when conditions are good, and the risk of continued indeterminate growth which may be followed by production of greater numbers of reproductive modules if conditions remain favourable. For example, *Floerkea proserpinacoides* (Limnanthaceae), a short-lived ephemeral, commits meristems to reproductive modules at an earlier stage of growth when crowded than when less crowded (Smith 1984). Extreme examples are provided by palms such as *Corphya alata* in which the inflorescence is terminal and flowering ends the life of the tree (Halle *et al.* 1978). However, many plants retain the potential for phenotypic plasticity by holding a substantial proportion of their meristems dormant, only allowing them to develop after stimulation by damage or other changes in the environment.

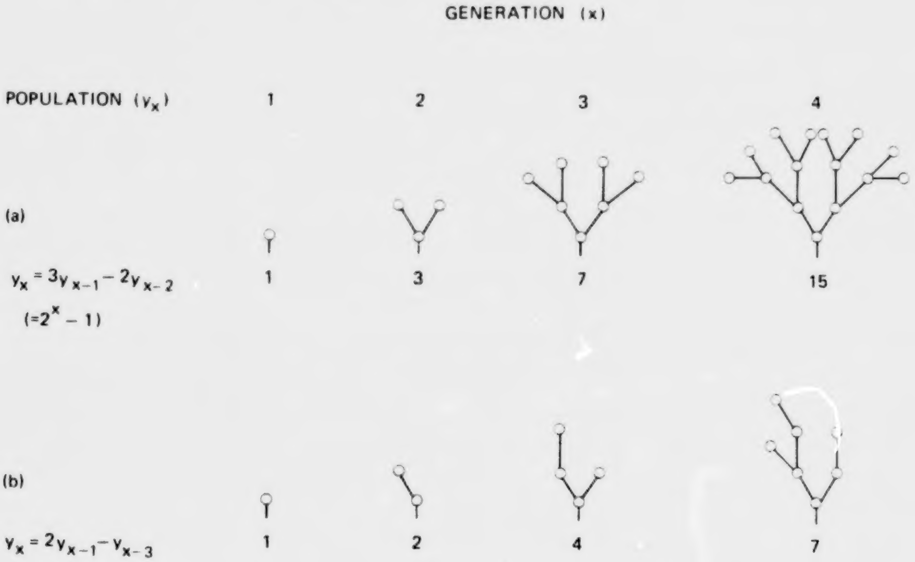

Fig. 1. Growth of populations of modules (y_x) in the first four module generations (x) compared for plants which branch by apical bifurcation (a) and by development of lateral buds one generation after apical buds (b). Relative growth rates stabilise 0.69 modules/mod./gen. for (a) and 0.49 mod./mod./gen. for (b).

In environments varying in space, there will be a similar tradeoff between committing currently available resources to reproduction allowing further vegetative extension which may encounter richer supplies of resources and allow greater reproductive effort later. The observed architectures of plants represent conservative, compromise, answers to these interlocking questions of action 'now or later' and 'here or elsewhere' facing all organisms in an uncertain world (Southwood 1977).

Architecture and Effects of Damage on Plant Populations

Herbivores and pathogens damage plants in a variety of ways but all probably affect the expression of architecture, either through direct removal of mature or developing modules or through removal of resources forcing plants to alter their priorities and timing for development of meristems. The changed expression of architecture can be used for comparing the effects of different kinds of attack in a way which relates numbers of herbivores to changes in a plant's potential for growth and reproduction.

The effects of damage can be assessed by measuring the proportions of meristems which develop into modules of particular types in particular intervals of time in the presence of the damaging factor acting at different intensities. The proportions, expressed as probabilities, can then be used to calculate effects on rates of change of populations of modules and ramets of the plant.

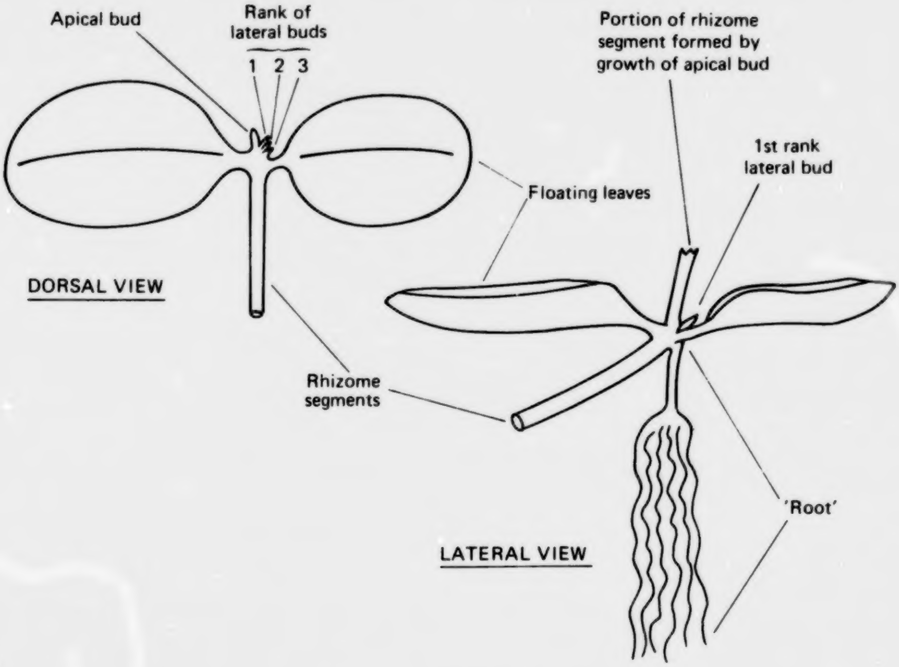

Fig. 2. Diagrammatic representations of ramets of *Salvinia molesta* D.S. Mitchell in which (dorsal view) the apical bud has yet to develop and (lateral view) the apical bud, but none of the lateral buds, has grown into a new ramet in continuation of the parent branch.

Salvinia molesta — A Simple Example

The floating fern *Salvinia molesta* D.S. Mitchell (Salviniaceae) has several characteristics which allow easy application of this architectural approach. There is no sexual reproduction and the entire species appears to be a single genet without variation due to genetic mutations. Having no gametophyte stage in the life cycle, population processes depend solely on growth and survival of vegetative parts. The rate of growth is very high under conditions close to optimal, allowing experiments to be conducted quickly. All parts of the plant are accessible without excavation, branching takes place in two rather than three dimensions and ramets are formed of a constant small number of parts.

Each ramet consists of a pair of leaves which float on the water surface, a dissected leaf which hangs below and functions as a root, and a horizontal segment of rhizome (Fig. 2). Each ramet initially bears an apical bud, which usually develops into a new ramet in continuation of the parent rhizome branch, and three lateral buds which can develop into the first ramets of new side-branches. The growth of buds gives rise to two-dimensional 'trees' of rhizomes which continue to grow distally while senescing and fragmenting proximally. The morphology and anatomy of ramets have been described by Bonnet (1955) and Croxdale (1978, 1979, 1981). In the present study, ramets were chosen as the modules of the plant's architecture because they are constructed of a constant number of parts.

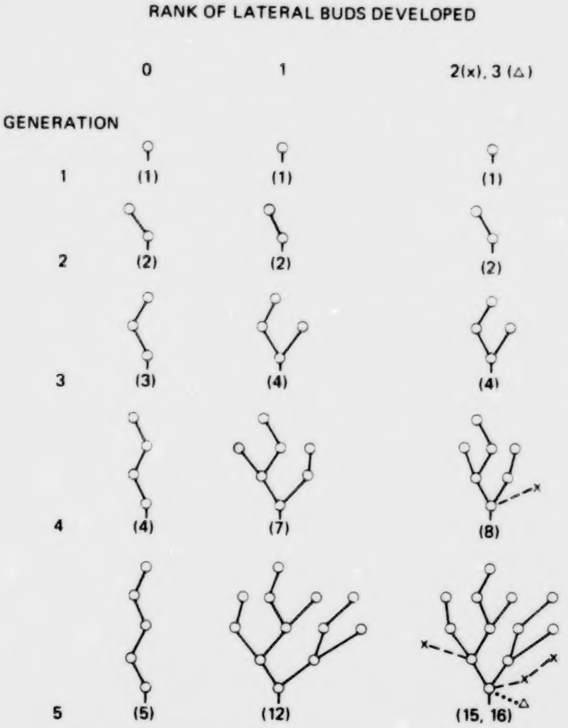

Fig. 3. Architecture of *Salvinia molesta* D.S. Mitchell: five ramet-generations of growth from a single ramet (○) with complete development of zero, first-, second- (x) and third- (△) rank lateral buds. Populations of ramets in each generation are shown in parentheses.

The rhizome architecture of *S. molesta* (Fig. 3) was investigated by mapping rhizomes connecting groups of ramets, referred to as colonies, collected from a range of conditions but having suffered no damage (Room 1983). Under conditions stimulating development of all lateral buds, there was a sequence of development in each ramet from apical to first- to second- to third-rank lateral buds, each separated in physiological time by one ramet generation. Second- and third-rank buds do not usually develop in natural waters and neither do all first-rank buds. Development of second- and third-rank buds occurred frequently in a sewage treatment lagoon and the branches which resulted followed the same rules of growth as branches arising from first-rank lateral buds. This appeared to be an example of adaptive reiteration (Bell and Tomlinson 1980) in which the basic architecture for first-rank branches was repeated under conditions 'better' than those which stimulate development of all first-rank buds.

A difference equation model was constructed (Appendix 1) which described growth in numbers of ramets for the cases of complete expression of first-, second- and third-rank branching (Fig. 3) (Room 1983). The model was extended to include loss of ramets due to senescence (Fig. 4), loss of ramets and individual buds due to damage, and the fission of colonies resulting from loss of ramets. The assumption of complete expression of any degree of branching was unrealistic, so a stochastic simulation model was also built which used age- and position-specific probabilities of bud development and a set of branching rules to generate intermediate degrees of branching. The simulation model included routines representing losses due to senescence and damage and compensation for damage. Its performance was checked for the special cases of complete first- and second-rank branching by comparison with the difference equation model. A graphics facility allowed maps of colonies grown and damaged by the simulation model to be displayed on a television monitor.

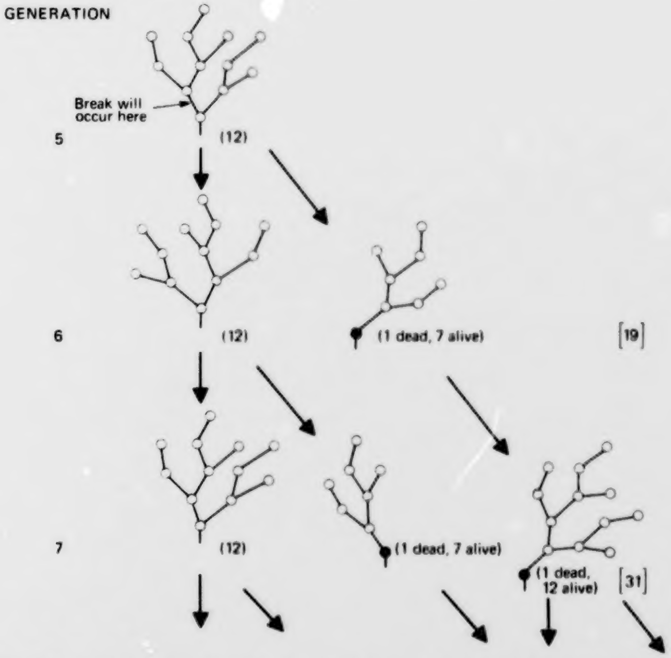

Fig. 4. Continued growth of the colony having complete development of first-rank lateral buds in Fig. 3 when ramets die at a constant age of five ramet-generations and colonies fragment as the dead rhizome segments break. Dead ramets are represented by solid circles, gross populations are shown in parentheses, and nett populations in square brackets.

The models were run with different percentages of buds alone being destroyed, and then with buds plus ramets being destroyed, and the effects on rates of change of populations of ramets and of colonies were calculated assuming no growth in compensation for damage (Fig. 5). During its lifetime, each ramet produces two new ramets for complete first-rank branching, or three new ramets for complete second-rank branching (Fig. 3). Ramets will simply replace themselves, rather than increasing their population, if 50% or 67% respectively of developing buds are destroyed as shown by curves *c* and *a* for $r = 0$ in Fig. 5. Probabilities of bud development in the field are usually less than 1.0 (Room 1983) and curves *e* and *f* show how destruction of buds alone depressed population increase for incomplete first-rank branching. The irregular shapes of curves *e* and *f* were due to the use of a random number generator which resulted in variation between the 50 colonies simulated for each point in the curves. Curve *d* shows that destruction in each generation of 44% of developing buds plus 22% of ramets less than three generations old should result in zero population growth under conditions otherwise stimulating complete first-rank branching.

The two biological control agents for *S. molesta* which have been released in Australia (Room *et al.* 1981, 1984) cause different kinds of damage to the plant. The weevil, *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae), causes most damage to buds and young sections of rhizomes, and larvae of the moth, *Samea multiplicalis* (Guenée) (Lepidoptera: Pyralidae), damage expanded leaves. Studies of the effects of the different kinds of damage are still in progress (Room *et al.* 1985) but preliminary results will be used below to show how numbers of insects can be related to reduced growth by the plant.

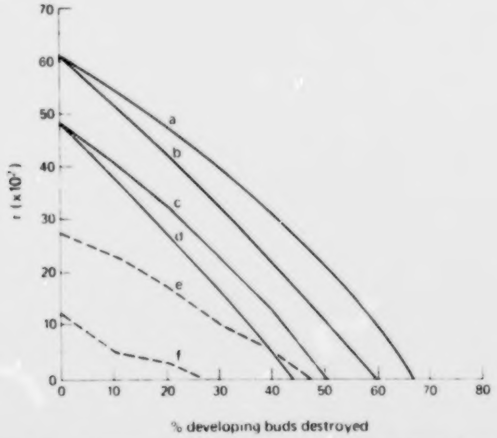

Fig. 5. Rates of ramet population increase (r) for *Salvinia molesta* D.S. Mitchell derived from the difference equation model (a to d) and simulation model (a to f): (a, c) complete first- and second-rank branching respectively, only buds destroyed; (b, d) as for (a, c) but with young ramets destroyed in addition to and at half the rate of, buds destroyed; (e, f) buds only destroyed when probabilities of development are 1.0 for apical buds and 0.2 and 0.03 respectively for first-rank lateral buds remaining.

Under conditions close to the optimum for the insects, it appears that *C. salviniae* adults each destroy about five buds (Forno and Bourne, pers. comm.) and their larvae each destroy about 1.2 rhizome segments (Sands *et al.* 1983) in one ramet generation of *S. molesta*. In the absence of compensation by the plant, 10 adults per 100 buds should result in destruction of 50% of buds and control of the weed in most conditions experienced in the field. Alternatively, 8.8 adults plus 18.3 larvae/100 buds should have the same effect by destroying 44% of buds plus 22% of young ramets.

In fact, the plant responds to destruction of buds, or ramets bearing buds, by increasing the probabilities of development of buds eligible to develop in the next ramet generation while keeping generation-time constant (M.H. Julien, pers. comm.). This seems to be a case of instantaneous compensation (Hearn and Room 1978) in which materials which would have been allocated to destroyed buds are redirected to remaining buds. The depression of ramet population increase by damage is reduced and the expression of architecture is changed, exhibited sometimes by the growth of second or higher rank branches where previously there were only first-rank branches. Making the simulation model compensate for damage by replacing each bud destroyed in one generation by a new bud in the next generation suggested that 67% of buds alone, or 60% of buds plus 30% of young ramets, should be destroyed to result in control of the weed. This level of damage should be caused by populations of 13.4 adults/100 developing buds in the case of buds only destroyed, or by 12 adults plus 25 larvae/100 developing buds in the case of buds and ramets destroyed. These estimates compare with maxima of *c.* 10 adults plus unknown numbers of larvae/100 buds observed just prior to rapid destruction of *S. molesta* mats in several lakes in Papua New Guinea (P.A. Thomas and P.M. Room, unpubl. data).

Preliminary studies of *S. multiplicalis* suggest that its damage increases the duration of each ramet-generation (L. Duivenvoorden, pers. comm.). The effect may be due to removal of photosynthetic area, or resources, and might result in the development of fewer buds than in undamaged plants. This could be simulated by reducing probabilities of bud development and increasing the duration of a ramet generation according to the population density of the insect and consequent severity of damage.

Discussion

The approach described here gives understanding of plant/herbivore interactions at a level intermediate between that given by physiological or chemical measurements and that given by measurements of weight, volume or area occupied by plants. Appropriate records can be made non-destructively, at least for above-ground parts, and the results allow the numbers of herbivores present at one time to be used to predict the numbers and types of plant modules present in the future.

By using probabilities of development in a series of time intervals, the technique can take into account the timing of damage and can be used to show how delays in growth caused by damage can reduce the competitiveness of individual plants. Unlike *S. molesta*, many plants have a seasonal cycle of reproduction which must be completed before physical conditions become unsuitable. For those plants, the timing of attack in relation to the time available for compensatory growth will be just as important as the ages, positions and numbers of modules damaged (Harris 1971; Hearn and Room 1978).

The architectures of plants are compromises resulting from past actions of sometimes opposing selective forces and architectures are unlikely to be expressed as optimal arrangements of modules for the exploitation of any particular circumstances. Further, the expression of architecture stimulated during early development might not be the most efficient for conditions experienced later. A common response to this situation is self-pruning, often seen for example in trees grown in dense plantations (Kozlowski 1973). It follows that damage of certain types at certain times could prune plants to give more efficient arrangements of modules, and hence more growth, of damaged compared with undamaged individuals (Harris 1974). However, such positive effects must have been small, or unpredictable, or there would have been selection for the architecture to be modified to give the same arrangement of modules without incurring the losses due to pruning.

Though the number and arrangement of modules is generally more plastic than their size, shape and chemical quality (Bradshaw 1965), there is variation among modules of the same type and this variation is suspected to be of great importance to plant–herbivore interactions (Denno and McClure 1983). The architectural approach outlined here could be used to place information on such variation, and associated patterns of damage, into the context of growth of whole ramets and populations of ramets. For example, modules containing higher concentrations of defensive chemicals might be less susceptible to attack but might also grow more slowly (Cates 1975; Whitham and Slobodchikoff 1981). The position, number and timing of appearance of such modules in relation to overall growth and the timing of attack should have significant effects on rates of change of plant populations which could be explored using architectural models.

Most plants have more complex morphologies and biologies than *S. molesta* and application to them of the architectural approach would require a greater investment of effort. However, Fisher and Honda (1979) and Maillette (1982*a*, *b*) have shown that even the structural dynamics of trees can be analysed and modelled in appropriate ways and there seems to be no alternative method for relating the position, nature and timing of damage, and effects of the environment, to growth and reproduction of plants. Could measuring probabilities of meristem development satisfy 'one of the most urgent needs in the biological control of weeds ... a method by which individual stresses on the target plant, whatever their origin, can be quantified in a common unit and summed' (Harris 1981)?

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Appendix 1

Computer Model of Biological Control of Salvinia

The following is a listing of a model which was demonstrated at the Symposium. The model is a simplified version of that described in this paper and it is written in BASIC for the Commodore 64 microcomputer. It uses the SCREEN-GRAPHICS-64 software package marketed by Abacus Software which must be wedged into the C-64 memory before the model is loaded.

The model grows branching rhizomes of salvinia on a TV screen, in colour, and shows old sections of rhizome being removed by senescence and younger sections and buds being removed by larvae and adults respectively of the biological control agent *Cyrtobagous salviniae*. Records of the input paramets being used and counts of the numbers of generations of growth, numbers of ramets and numbers of colonies present are shown in the corners of the screen. Sound effects are used to distinguish between birth and death of ramets and to indicate when biological control has been achieved. A menu enables initialisation with parameters such as the longevity of undamaged ramets and probabilities of attack by adults and larvae of *C. salviniae*. Note that special Commodore characters controlling spacing in PRINT and INPUT statements in lines 6 to 55 could not be shown in this listing and the menu will appear crowded unless those characters are added.

```
0 REM:       SALVINIA
1 REM: RA(NO,V) V=1ANGLE, 2X, 3Y, 4AGE, 5FROM, 6TOMAIN, 7TO1ST, 8RIGHT/LEFT
2 REM:
5 M=100:DIMRAM(M,8):S=54272:S1=S+1:S2=S+4:S3=S+5:S4=S+15:S5=S+24
6 PRINT"          SALVINIA RHIZOME MODEL":PRINT"  PRESS RETURN FOR DEFAULT OPTIONS"
7 INPUT"RAMET LIFESPAN (RAMET GENERATIONS)  4";MA:MA=MA+2
8 INPUT"LATERAL BUD DELAY (RAMET GENS.)  1";AB
9 INPUT"APICAL & LATERAL ANGLES(RADIANS)  .6,.7";T,TB
10 SA$="L.ANGLE"+STR$(TB):SM$="A.ANGLE"+STR$(T):OA$="R. LIFE"+STR$(MA-2)
11 BG$="L.DELAY"+STR$(AB):LPOP=0
```

```
12 INPUT"APICAL & LAT. PROBABILITIES  1,1";PM,PB:PM$="A.PROB"+STR$(PM)
13 INPUT"% BUDS & RAMETS DESTROYED  0,0";B%,R%:BD$="%BUD D"+STR$(B%)
14 PB$="L.PROB"+STR$(PB):R$="%RAM D"+STR$(R%)
18 INPUT"LENGTH OF RHIZOME SEGMENT(00;10-35)  35";R
19 IFR=0THEN6
20 Q=R/7:NX=2:CL=0:ZZ=0:DD=0:LPOP=0
40 PRINT"           RUN CONTROLS":PRINT"         * FOR CONTINUOUS RUN"
42 FRINT"         A TO ABORT RUN"
45 PRINT"         R TO RESET":PRINT"         F5 MEANS PRESS FUNCTION 5"
50 FORI=0TO500:NEXTI:FORI=1TONR+5:FORJ=1TO8:RA(I,J)=0:NEXT:NEXT:RA(0,4)=99
55 PRINT"           PRESS BAR TO START":C$=""
60 GETA$:IFA$=""THEN60
75 PRINT"":NR=1:NW=1:HIRES6,10
77 CHAR1,1,198,7,"GENERATION":CHAR1,1,190,7,"NO RAMETS"
80 CHAR1,1,182,7,"NO COLONIES":CHAR1,1,174,7,"RGR RAMETS"
82 CHAR1,1,8,1,SA$:CHAR1,1,16,1,SM$:CHAR1,1,24,1,BG$:CHAR1,1,32,1,OA$
85 CHAR1,245,8,1,R$:CHAR1,245,16,1,BD$:CHAR1,245,24,1,PB$:CHAR1,245,32,1,PM$
88 RAM(1,1)=T/2:RAM(1,2)=160:RAM(1,3)=90-2*R:RAM(1,8)=1:RAM(1,4)=2:ZA=0
90 CIRCLERAM(1,2),RAM(1,3),Q,1:DRAWRAM(1,2),RAM(1,3),RAM(1,2),RAM(1,3)-R/3,1
95 COPY1,2000:COPY2,3000:COPY3,4000:SPRITE1,1,0,0,0,0,7:SPRITE3,3,0,0,0,0,2
96 IFB%<>0THEN:PLACE1,235,26
97 IFR%<>0THEN:PLACE3,235,20
130 REM:
131 REM:   GENERATION AND RAMET LOOPS
132 FORZ=1TO99:FORN=1TONW:IFN=1THEN140
134 REM:    DESTROYS NEW RAMETS
135 IFRAM(N,4)<3ANDR%>100*RND(1)THENRAM(N,7)=999:RAM(N,6)=999:GOTO180
140 IFRAM(N,4)>MATHEN180
141 IFRAM(N,6)=0THENTY=0:GOTO150
142 IFRAM(N,7)>0THEN180
143 IFRAM(N,4)<AB+2THEN180
145 TY=1:GOTO152
150 IFPM>RND(1)THEN160
151 GOTO180
152 IFPB>RND(1)THEN160
153 GOTO180
154 REM:    DESTROYS BUDS
160 IFRA(N,6+TY)=998THEN170
163 IFB%>100*RND(1)THENRA(N,6+TY)=998:PLACE1,RA(N,2)+12,RA(N,3)+19+Q:
    GOSUB1200:GOTO170
168 GOSUB500:IFZZ=1THEN14
170 IFAB=0ANDTY=0THEN145
180 NEXTN:NW=NR:GOSUB600:IFZA=1THEN18
185 POP=NR-DD:IFPOP=0ORLPOP=0THENRGR=0:GOTO189
187 RGR=INT(100*(LOG(POP)-LOG(LPOP)))/100
189 CHAR1,90,198,2,STR$(Z):CHAR1,90,190,2,STR$(POP):CHAR1,90,182,2,STR$(CL+1)
190 CHAR1,82,174,2,STR$(RGR):CHAR1,245,198,2,"PRESS BAR"
191 IFC$="*"THEN193
192 GETC$:IFC$=""THEN192
193 IFC$="A"THEN:NORM:GOTO14
194 IFC$="R"THEN:NORM:GOTO6
196 LPOP=POP:MODE1:CHAR1,245,198,2,"PRESS BAR"
197 CHAR1,90,198,2,STR$(Z):CHAR1,90,190,2,STR$(POP):CHAR1,90,182,2,STR$(CL+1)
198 CHAR1,82,174,2,STR$(RGR)
200 MODE0:NEXTZ:END
499 REM:
500 REM: FINDS NEW ANGLES AND POSITIONS
510 X=RAM(N,2):Y=RAM(N,3):IFTY=1THENRAM(N,1)=RAM(N,1)-2*RAM(N,8)*TB
520 C=RAM(N,8)*-1:X1=X+R*SIN(RAM(N,1)):Y1=Y+R*COS(RAM(N,1))
525 GOSUB1000:IFZZ=1THENRETURN
```

```
528 NR=NR+1:IFNR>MTHEN:CHAR1,170,190,2,"ARRAY EXCEEDED: F5":END
529 RAM(NR,4)=1:RAM(NR,5)=N
530 RAM(NR,1)=RAM(N,1)+(C*T):RAM(NR,2)=X1:RAM(NR,3)=Y1
535 IFTY=0THENRAM(N,6)=NR:RAM(NR,8)=C:GOTO550
540 RAM(N,7)=NR:RAM(NR,1)=RAM(N,1)+(-1*C*T):RAM(NR,8)=-1*C
550 RETURN
599 REM:
600 REM: INCREMENTS AGES
610 FORN=1TOM:IFRAM(N,4)=0THENRETURN
620 IFRAM(N,4)=99THEN800
625 IFR<30THEN631
630 MODE1:CHAR1,RAM(N,2),RAM(N,3),1,STR$(RAM(N,4)-2)
631 IFRAM(N,7)=999THEN:PLACE3,RA(N,2)+12,RA(N,3)+12:GOSUB1300:GOTO640
635 RAM(N,4)=RAM(N,4)+1:IFRAM(N,4)<MATHEN780
640 RA(N,4)=99:MODE1:CIRCLERA(N,2),RA(N,3),Q,1:DOTRA(N,2),RA(N,3),1
650 FORU=15TO5STEP-1:POKES5,U:POKES2,129:POKES3,15:POKES1,40:POKES,200:
    NEXT:POKES2,0:POKES3,0
660 IFN=1THEN675
670 TX=RAM(RAM(N,5),2):TY=RAM(RAM(N,5),3):DRAWRA(N,2),RA(N,3),TX,TY,1:GOTO680
675 DRAWRAM(1,2),RAM(1,3),RAM(1,2),RAM(1,3)-R/3,1
680 MODE0:DD=DD+1:T1=RAM(N,5):T2=RAM(N,6):T3=RAM(N,7):IFT2>996ORT3>996THEN750
682 IFRA(T1,4)=99ANDN<>1THEN700
683 IFT2=0ANDT3=0THENCL=CL-1:GOTO760
684 IFT2=0ORT3=0THEN800
685 IFRA(T2,4)=99ANDRA(T3,4)=99THENCL=CL-1:GOTO760
686 IFRA(T2,4)=99ORRA(T3,4)=99THEN800
688 CL=CL+1:GOTO800
692 IFRAM(T2,4)=99ANDRAM(T3,4)=99THENCL=CL-1:GOTO760
700 IFT2=0ANDT3=0THENCL=CL-1:GOTO760
710 IFT2=0ANDRA(T3,4)=99THENCL=CL-1:GOTO760
720 IFT3=0ANDRA(T2,4)=99THENCL=CL-1:GOTO760
725 IFRA(T2,4)=99ANDRA(T3,4)=99THENCL=CL-1:GOTO760
730 IFT2>0ANDRA(T2,4)<>99THEN:IFT3>0ANDRA(T3,4)<>99THENCL=CL+1
740 GOTO800
750 IFRA(T1,4)<>99THEN800
752 IFT2=999ORT3=999THENCL=CL-1:GOTO760
754 IFT2=998ANDT3=998THENCL=CL-1:GOTO760
756 IFT3<>998THEN:IFT2=998ANDRA(T3,4)=99THENCL=CL-1:GOTO760
758 IFT2<>998THEN:IFT3=998ANDRA(T2,4)=99THENCL=CL-1:GOTO760
759 GOTO800
760 IFCL<0THEN:CHAR1,120,110,3,"EXTINCT!  F5":ZA=1:GOSUB900:RETURN
770 GOTO800
780 MODE0:IFR<30THEN800
790 CHAR1,RAM(N,2),RAM(N,3),1,STR$(RAM(N,4)-2)
800 NEXTN
900 REM:    EXTINCTION SOUND
902 IFR%=0ANDB%=0THEN906
905 OFF1:OFF3:SPRITE2,2,0,0,0,0,7:PLACE2,160,100
906 FORV=54272TO54296:POKEV,0:NEXTV
910 POKES5,15:POKES3,15:POKES+6,16:POKES1,38:POKES,126:POKES2,17
920 FORI=50TO250STEP5:POKES1,I:POKES,I-50:NEXT
930 FORI=200TO50STEP-4:POKES1,I:POKES,I-50:NEXT
940 POKES1,34:POKES,75:FORI=0TO100:NEXT
950 POKES2,0:POKES3,0:POKES+6,0:POKES5,0:RETURN
999 REM:
1000 REM: CREATES NEW RAMET
1010 IFX1>320-QTHEN1030
1011 IFX1<QTHEN1030
1012 IFY1>200-QTHEN1030
1013 IFY1<QTHEN1030
```

```
1015 GOTO1050
1020 IFY1<190ANDY1>QTHEN1050
1030 CHAR1,190,190,2,"OUT OF SPACE: F5":ZZ=1:RETURN
1050 DRAWX,Y,X1,Y1,1:CIRCLEX1,Y1,Q,1
1060 POKES1,130:POKES3,9:POKES4,30:POKES5,15:POKES2,21:FORUQ=1TO70
1070 NEXT:POKES2,20:POKES5,0:RETURN
1199 REM: ADULT SOUND
1200 FORV=54272TO54296:POKEV,0:NEXTV
1210 POKES5,15:POKES3,15:POKES+6,16:POKES1,38:POKES,126:POKES2,17
1220 FORI=50TO250STEP5:POKES1,I:POKES,I-50:NEXT
1250 POKES2,0:POKES3,0:POKES+6,0:POKES5,0:RETURN
1299 REM: LARVA SOUND
1300 FORU=20TO5STEP-1:POKES5,U:POKES2,33:POKES3,15:POKES1,40:POKES,200:
     NEXT:POKES2,0:POKES3,0
1310 RETURN
1999 REM:    WEEVIL SPRITE
2000 BIT"000000000000000000000000"
2001 BIT"000000000000000000000000"
2002 BIT"000000000000000111100000"
2003 BIT"000000000000011111111000"
2004 BIT"111000110110111111111100"
2005 BIT"000100101111111111111110"
2006 BIT"000011110111111111111110"
2007 BIT"000011000101101111111111"
2008 BIT"000110001000010111111111"
2009 BIT"000000010000010000010011"
2010 BIT"000000100000010001000000"
2011 BIT"000000100000010001000000"
2012 BIT"000001100000011001110000"
2013 BIT"000000000000000000000000"
2014 BIT"000000000000000000000000"
2015 BIT"000000000000000000000000"
2016 BIT"000000000000000000000000"
2017 BIT"000000000000000000000000"
2018 BIT"000000000000000000000000"
2019 BIT"000000000000000000000000"
2020 BIT"000000000000000000000000"
2999 REM:    DEAD WEEVIL SPRITE
3000 BIT"000000000000000000000000"
3001 BIT"000000000000000000000000"
3002 BIT"001100110011011000000000"
3003 BIT"001100110001101100000000"
3004 BIT"001101100001100011000000"
3005 BIT"111101100000110001100000"
3006 BIT"111000110000011011000000"
3007 BIT"011100011001100110011100"
3008 BIT"001110011110011111111110"
3009 BIT"000011111111111111111111"
3010 BIT"000011111111111111111111"
3011 BIT"000001101100111111111110"
3012 BIT"000000000000111111111100"
3013 BIT"000000000000000111110000"
3014 BIT"000000000000000000000000"
3015 BIT"000000000000000000000000"
3016 BIT"000000000000000000000000"
3017 BIT"000000000000000000000000"
3018 BIT"000000000000000000000000"
3019 BIT"000000000000000000000000"
3020 BIT"000000000000000000000000"
3999 REM:    LARVA SPRITE
```

```
4000 BIT"000000000000000000000000"
4001 BIT"000000000000000000000000"
4002 BIT"000000000000000000000000"
4003 BIT"000000000000000000000000"
4004 BIT"000000000000000000000000"
4005 BIT"000000000000000000000000"
4006 BIT"000000000000000000000000"
4007 BIT"000000000000000000000000"
4008 BIT"000000000111111000000000"
4009 BIT"000000011111111111000000"
4010 BIT"000000111111111111110000"
4011 BIT"000001111111111111111100"
4012 BIT"000001111110000000001111"
4013 BIT"000001111000000000000011"
4014 BIT"000000000000000000000000"
4015 BIT"000000000000000000000000"
4016 BIT"000000000000000000000000"
4017 BIT"000000000000000000000000"
4018 BIT"000000000000000000000000"
4019 BIT"000000000000000000000000"
4020 BIT"000000000000000000000000"
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Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 103-19 (1985)

The Search for Effective Biological Control Agents in Europe
1. Diffuse and Spotted Knapweed

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Abstract

The difficulties experienced during foreign exploration in the search for safe and effective biological control agents are discussed for diffuse and spotted knapweed (*Centaurea diffusa* and *C. maculosa*, respectively). Apart from unsolved taxonomic problems in case of spotted knapweed, field surveys were handicapped by the fact that the optimal survey area was not accessible and that both target weed species were of scattered occurrence in the marginal areas surveyed. Well-developed complexes of specific natural enemies were not found and the effect of individual species on the distribution and abundance of their host plants could not be studied in the field because of low densities of plants and natural enemies. However, the field surveys were still rewarding. Information is given on 23 species of potential control agents, six of which have already been released in North America. Attention is called to the increasing demands for safety specifications for potential control agents of diffuse and spotted knapweed. It is proposed to assess these demands carefully.

Choix d'Agents Efficaces de Lutte Biologique — Possibilités et Facteurs Limitatifs Généraux

Compte tenu du temps et des sommes qu'il faut consacrer aux études sur le terrain et aux essais de spécificité d'hôtes, on propose de choisir des agents biologiques apparemment efficaces après l'étude de la documentation générale et des enquêtes sur le terrain dans des régions appropriées. Le rapport traite des difficultés suscitées à cet égard par les chercheurs ailleurs en Europe et cite comme exemple les recherches sur *Euphorbia* et *Centaurea*. On accorde une attention particulière aux aspects tels l'accessibilité de zones d'étude appropriées, la répartition et l'abondance des plantes hôtes, la présence et l'abondance d'organismes bien adaptés pouvant potentiellement jouer le rôle d'agents biologiques ainsi que les problèmes techniques qui se posent. L'auteur montre qu'il est souvent difficile de déterminer l'efficacité des organismes associés à la plante nuisible cible dans son aire de répartition indigène ou de recueillir un nombre suffisant d'échantillons en vue des études en laboratoire. En outre, il parle de certains problèmes qui se posent dans le choix d'agents biologiques potentiellement efficaces, comme l'aire de distribution des plantes hôtes, les conflits d'intérêts en ce qui concerne le lieu d'introduction et la question des espèces de plantes indigènes rares et menacées de disparition. Il précise qu'il faut parfois éliminer certains agents biologiques appropriés et efficaces en raison de facteurs limitatifs inhérents à la lutte biologique.

Introduction

Alien weeds, established by accident or design, usually are introduced without their specific natural enemies, i.e. phytophagous arthropods and phytopathogens (Goeden 1971, 1974; Maw 1976). Foreign exploration in the weed's native range for suitable and effective control agents is therefore a major part of each classical biological control project. Before foreign exploration is started, it is indispensible to determine the identity and taxonomic position of the target weed, collect information on its origin and the history of its introduction and distribution, as well as on the arthropods and pathogens associated with the weed throughout the colonized area.

Surveys for safe and potentially effective biological control agents should preferably be carried out in the area of greatest diversification of the genus or subgenus to which the target weed belongs (Wapshere 1974*a*, 1981). A second guideline for selecting the survey area is that it should be climatically similar to the region where the weed occurs at noxious levels (Wapshere 1981).

Another important consideration in foreign exploration is the early selection of potentially effective control agents. Proposals on how these agents can be selected are given by Harris (1973), Wapshere (1974*b*), and Goeden (1983).

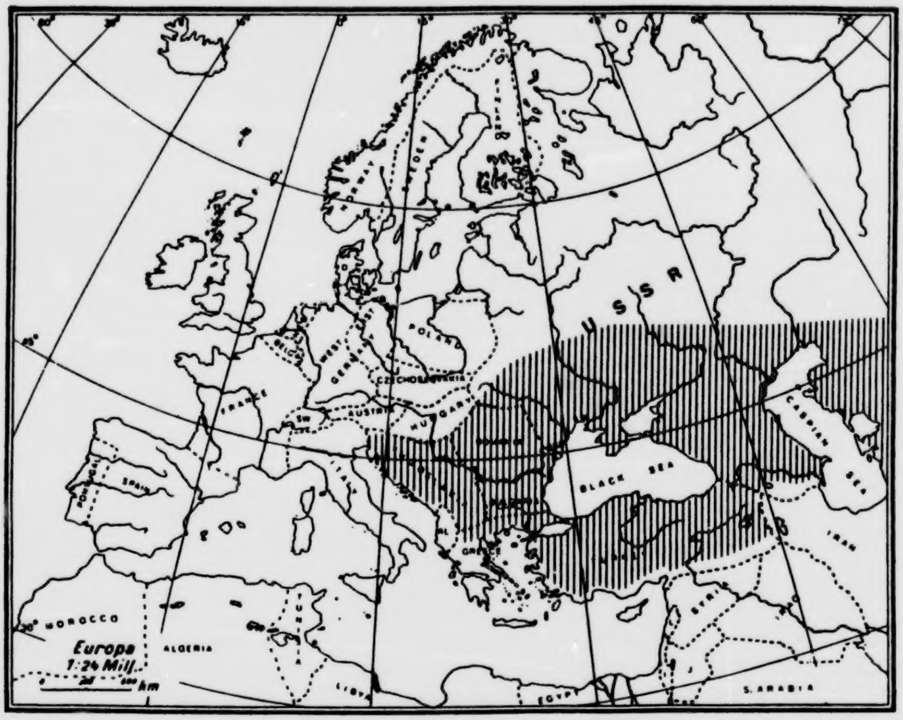

Fig. 1. Geographic distribution of *Centaurea diffusa* Lam. in Europe (Dostal 1976).

Some of the difficulties experienced during foreign exploration to follow these scientifically sound demands will be illustrated and discussed in this paper, using work in Europe on diffuse and spotted knapweed as examples.

The Taxonomy of Diffuse and Spotted Knapweed

The genus *Centaurea* (Compositae) consists of around 500 predominantly Mediterranean species. Diffuse knapweed, *Centaurea diffusa* Lam., is taxonomically well defined, and North American and European plants seem to belong to the same species. The spotted knapweed of North America is usually identified as *C. maculosa* Lam. (Moore and Frankton 1974). *C. maculosa* belongs to the difficult and poorly studied *C. paniculata* L. group of about 30 species with many transitional forms and hybrids

(Landoldt *et al.* 1972). There is little consensus how this group should be treated and the specific characters used are poorly defined and plastic. The treatment by Dostal (1976) lists 13 species and 15 subspecies in the section Maculosae that are widely distributed over Europe. *C. maculosa* in this treatment is a diploid ($2n = 18$) biennial found from central France to south Germany and northern Italy. The North American spotted knapweed is a perennial tetraploid ($2n = 36$) and is found in a much drier climate. Moore and Frankton (1974) equated the North American species with *C. stoebe* L. and *C. maculosa* ssp. *rhenana* (Boreau) Gugler which is treated by Dostal (1976) as *C. rhenana* Boreau. It is also a diploid ($2n = 18$) biennial extending from southeast Europe to central Russia. The best fit in Flora Europaea (Dostal 1976) is *C. biebersteinii* DC., which is a biennial or perennial tetraploid ($2n = 36$) that occurs in Albania, Bulgaria, Czechoslovakia, Hungary, Romania and Russia. Plants collected in this region by CIBC were identified as *C. micranthos* S.G. Gmeln ex Hayek or *C. maculosa* var. *micranthos*. This according to Dostal (1976) is a synonym for *C. biebersteinii* ssp. *biebersteinii*. However, all the plants collected from the region (mainly Hungary) were diploid ($2n = 18$) except for those from the Botanic Gardens, Cluj (Romania) which were tetraploid ($2n = 36$). It is now almost certain that because of different taxonomic treatments of spotted knapweed in Europe and North America, the problem species of British Columbia and the northwestern States of the United States has been largely missed in the surveys done in Europe for potential biological control agents.

The Selection of Suitable Survey Areas

The Distribution of Diffuse and Spotted Knapweed

The present distribution of *C. diffusa* in Europe and western Asia is shown in Fig. 1. Diffuse knapweed is a typical plant of the steppe vegetation in southern Russia and western Asia. Popova (1960) reported that in the Crimea it is a serious problem in dryland alfalfa, where it comprises 40–65% of the stands. West of the USSR it is only common and relatively abundant in the former steppe area in Dobrugea (Romania) and in northwestern Turkey. In Bulgaria, northern Greece and Yugoslavia it occurs as widely scattered patches. Small naturalized stands occur along the Adriatic coast of Yugoslavia, in southern France (Apt) and southwestern Germany (Karlsruhe).

In North America, the species was first recorded in Washington State in 1907 (Howell 1959) from where it spread into British Columbia (Groh 1943). Presently diffuse knapweed infests some 26 000 ha in British Columbia, as well as small areas in Alberta, Saskatchewan and Manitoba (Harris and Myers 1984). In the United States, *C. diffusa* occurs in Montana, Washington, Idaho, Oregon and California (Maddox 1982). It is suspected that first introductions were with alfalfa seed from Turkmenistan, USSR.

The distribution of the Eurasian *C. maculosa* group of species is given in Fig. 2. According to Dostal (1976) *C. rhenana* is the most widely distributed species, followed by *C. biebersteinii* ssp. *biebersteinii*, whilst *C. maculosa* spp. *maculosa* occurs only within the western part of the *C. rhenana* distribution range. A fourth species, *C. vallesiaca* (DC.) Jordan, is locally found in the western Alps. With the exception of some areas in eastern Austria and northwestern Hungary, spotted knapweed occurs in low density as widely scattered patches throughout its European distribution area. No information is available on the occurrence and abundance of spotted knapweed(s), especially of the tetraploid *C. biebersteinii* ssp. *biebersteinii*, in the USSR. All western collections of this species are diploid, with the exception of plants, although of unknown origin, in the Botanic Gardens Cluj (Romania). It cannot be excluded that the tetraploid *C.*

biebersteinii ssp. *biebersteinii* is restricted in distribution to the southern USSR, and the seeds first imported accidentally into North America originated from this area.

Groh (1943) reported that spotted knapweed was first collected in North America at Victoria, British Columbia in 1883. At present it infests some 2 500 ha in British Columbia, is common in Ontario, Quebec, and the Maritimes (Frankton and Mulligan 1970), and there are some small stands in Alberta (Watson and Renney 1974). However, the main infestations of more than 1 million ha are in Montana (800 000 ha), Idaho, Washington and Oregon, U.S.A. (Maddox 1982).

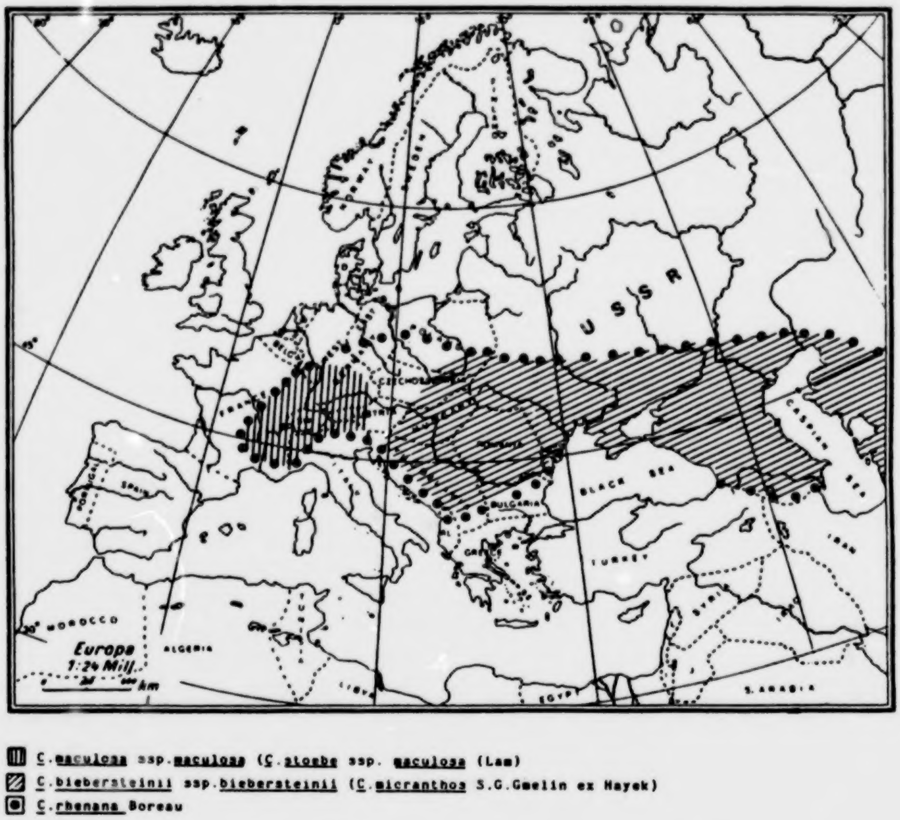
U S S R
BLACK SEA
CASPIAN SEA
BULGARIA
TURKEY
IRAN
SPAIN
MOROCCO
ALGERIA
LIBYA
EGYPT
S. ARABIA
Europe
1:24 Mill.
km
▥ C.maculosa ssp.maculosa (C.stoebe ssp. maculosa (Lam)
▨ C.biebersteinii ssp.biebersteinii (C.micranthos S.G.Gmelin ex Hayek)
● C.rhenana Boreau

Fig. 2. Geographic distribution of 3 taxa of the *Centaurea maculosa* group of species in Europe (Dostal 1976).

Based on the above information and the generally accepted guidelines for the selection of optimal survey areas, surveys for safe and potentially effective control agents for both diffuse and spotted knapweed should have been started in the southern USSR. This is also indicated by a comparison of the climatic diagrams (Walter and Lieth 1960) for the southern USSR and most of the area infested by the two knapweeds in North America. The climate in areas west of the Russian border differs in precipitation and temperature from the climate in most North American knapweed infestations. An exception is the Dobrugea area in eastern Romania which has an almost identical climate to the greater part of the area infested by spotted knapweed in Montana, U.S.A.

Field Surveys in Europe

Surveys by the European Station, CIBC, were started in 1961 in the western part of the European *C. maculosa* (*C. rhenana*) distribution area. This was justified for the following reasons: (*a*) the apparently optimal survey area in southern USSR was not accessible (which still applies); (*b*) the North American spotted knapweed was equated with *C. maculosa* ssp. *rhenana*; and (*c*) because of certain financial constraints. Between 1961 and 1964 some 40 *C. maculosa* sites were surveyed in France, Switzerland, southern Germany and eastern Austria (Zwölfer 1965). From 1965 onwards the survey was extended to eastern central Europe (Czechoslovakia and Hungary) and the Balkans (Yugoslavia, northern Greece, western Turkey, Bulgaria and Romania) to include the European distribution of *C. diffusa*.

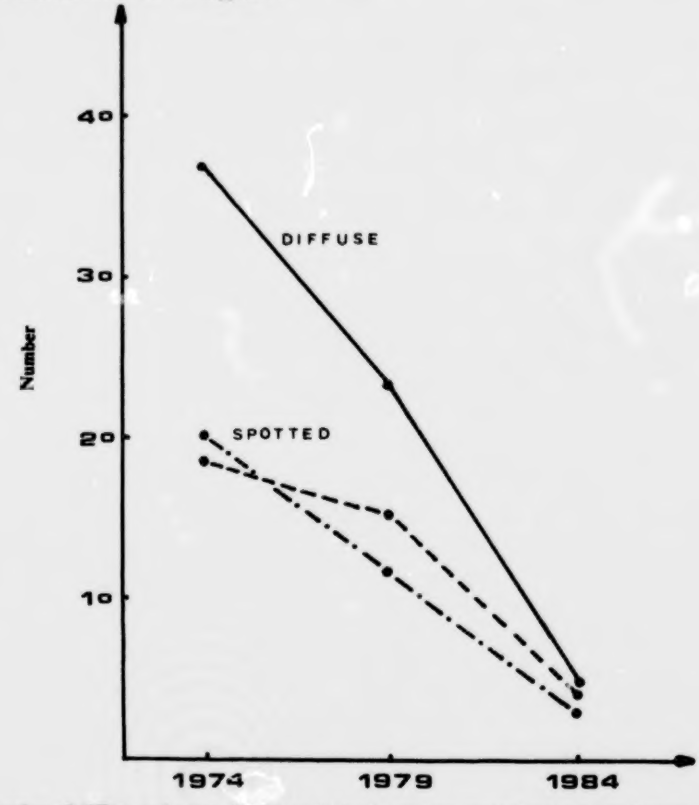

Fig. 3. Number of diffuse and spotted knapweed sites in western, central and eastern Europe, 1974–1984.

It was found that diffuse and spotted knapweed in Europe predominantly occur on ruderal sites (wasteland, gravel pits, quarries, roadsides, embankments, etc.) and only rarely in semi-natural habitats, such as dry, south-exposed slopes in vine-growing areas (*C. maculosa*) or permanent sheep pasture on shallow, gravel soils (*C. diffusa*). Although plant density and total number of plants were low at many of the ruderal sites, both knapweeds were relatively common in most of the survey areas when the survey was started. As shown in Fig. 3, this has drastically changed during the past 10 years. In addition to the decrease in number of sites, plant density has also decreased and stands with more than 500 plants are actually very rare.

Table 1. List of specific and oligophagous biotic agents attacking *Centaurea* spp. in Europe.

Biotic agent	Part attacked	*C. maculosa*	*C. diffusa*	Other *Centaurea* spp.
Fungi, Pucciniaceae				
Puccinia centaureae DC.	L	+	+	○
P. c. var. *diffusae* Savile	L	-	○	-
P. jaceae Otth.	L	+	+	○
P. j. var. *diffusae* Savile	L	-	○	-
Acarina, Eriophyidae				
Aceria centaureae (Nal.)	L	+	+	○
A. grandis (Nal.)	F	+	-	○
Aphidoidea, Aphididae				
Chomaphis centaureae CB.	R	○	-	○
Dactynotus jaceae (L.) ssp.				
D. reticulata HRL.	Sh(L)	○	-	-
Macrosiphoniella stägeri HRL.	Sh(L)	○	-	-
Protaphis alexandrea (Nevs)	Sh(L)	○	+	○
Trama centaureae CB.	R	○	+	○
Lepidoptera, Tortricidae				
Epiblema scutulana (Den. & Schiff.)*	F/Sh	○	-	○
Pelochrista medullana Zeller	R	+	+	○
Lepidoptera, Cochylidae				
Agapeta zoegana L.	R	+	-	○
Cochylis posterana Zeller*	F/Se	+	-	○
Stenodes alternana (Steph.)	F/Se	+	+	○
S. meridiana Stgr.	R	+	-	○
S. perfusana (Guen.)	F/Se	○	-	○
S. straminea (Haw.)	F/Sh	+	+	○
Lepidoptera, Gelechiidae				
Depressaria arenella Schiff.*	L	-	+	○
Metzneria diffusella Englert	F/Se	-	+	-
M. paucipunctella Zeller	F/Se	+	-	-
Pterolonche inspersa Stgr.	R	+	+	-
Lepidoptera, Nymphalidae				
Melitea ?phoebe Knoch*	L	-	+	○
Lepidoptera, Momphidae				
Pyroderces agyrogrammos Zeller*	F/Se	+	+	+
Diptera, Agromyzidae				
?*Melanagromyza aeneiventris* (Fallén)*	Sh/R	-	+	○
Diptera, Anthomyiidae				
Pegohylemyia centaureae Hennig	CB	+	+	-
Diptera, Cecidomyiidae				
Loewiola centaureae (F.Lw.)	L	○	-	○
Clinodiplosis cilicrus Kieff.	F	-	+	-
Diptera, Sciaridae				
Sciarid species	R?	+	+	-
Diptera, Syrphidae				
Cheilosia sp.	R	+	-	-

Table 1 *(continued)*

Biotic agent	Part attacked	*C. maculosa*	*C. diffusa*	Other *Centaurea* spp.
Diptera, Trypetidae				
Acanthiophilus helianthi Rossi*	F/Se	+	+	○
Chaetorellia nr. *hexachaeta* Loew.	F/Se	+	+	?
C. jaceae R.D.	F/Se	+	−	○
Chaetostomella onotrophes Loew.*	F/Se	+	−	○
Terellia virens Loew.*	F/Se	(+)	(+)	−
Urophora affinis Frfld.	F/Se	+	+	○
U. quadrifasciata Meigen	F/Se	+	+	○
U. algira Macqu.	F/Se	+	+	○
Hymenoptera, Cynipidae				
Isolcus nr. *jaceae* (Schenk.)	Se	+	+	○
Phanacis centaureae (Foerst.)	Sh	+	+	○
Coleoptera, Curculionidae				
Apion onopordi Kirby	Sh/R	+	+	○
A. orientale Gersch.	Sh/R	+	−	○
A. penetrans Germar	Sh/R	+	+	○
Cleonus piger Scop.*	R	+	+	○
Cyphocleonus achates Fab.	R	+	+	○
C. tigrinus Panzer*	R	+?	+?	○
Larinus australis Cap.	F	+	−	○
L. minutus Gyll.	F	−	+	−
L. obtusus Gyll.	F	+	−	○
L. sturnus Schaller*	F	+	−	○
Coleoptera, Buprestidae				
Sphenoptera jugoslavica Ob.	R	−	+	?+
Coleoptera, Chrysomelidae				
Arima marginata F.*	L	−	L	+
Cassida pannonica Suff.	L	+	−	−
C. vibex L.(?)	L	−	+	○
Chrysomela fuliginosa Ol.*	L	+	−	○
Sphaeroderma rubidum (Graells.)*	L	−	+	+
Coleoptera, Anobiidae				
Lasioderma redtenbacheri Bach.	Se	+	+	○
Coleoptera, Mordellidae				
Mordelistena sp.	Sh	−	+	−

○, literature record; +, survey record; −, not recorded; *, known to attack other Cynareae.

Plant part attacked: cB, central bud of rosette; F, flower; L, leaf; R, root collar and root; Se, seed; Sh, shoot.

Human activities have been responsible for this rapid loss in number of suitable knapweed sites. The main culprits have been the direct application of herbicides as well as herbicide drift from nearby intensive cultivation, as well as burning and cutting along roadsides, embankments and other such wasteland. In addition, new residential and industrial construction destroyed many former spotted knapweed sites in the Rhine Valley and in eastern Austria, and the transformation of uncultivated, unimproved pastureland into vineyards, as now occurs in Bulgaria and mainly Romania, has taken a toll of prime diffuse knapweed areas. Consequently surveys for additional control agents become increasingly more difficult and require a higher investment than previously. Under these circumstances, the demand to concentrate field surveys on 'optimal' survey areas cannot any longer be fulfilled. Surveys have to be made wherever knapweed can still be found.

Biotic Agents Associated with Diffuse and Spotted Knapweed in Europe

According to a literature review and information obtained from collections and specialists in Europe the two knapweeds are attacked by 53 species of biotic agents. These include 2 species of rust, 2 mites and 49 insects (Table 1). Fourteen of the insect species recorded attack other Compositae in addition to *Centaurea* spp. During field surveys by the European Station, CIBC, and the USDA Biological Control of Weeds Laboratory, Rome, 2 fungal, 2 mite and 34 insect species were found on spotted knapweed, and 2 fungal, 1 mite and 34 insect species on diffuse knapweed.

Table 2. Exploitation of specific food niches on diffuse and spotted knapweed by biotic agents[1] in Europe.

	Flowers seeds	Leaves	Shoots	Root collar root	Total	%
Centaurea maculosa						
Lepidoptera	7	—	2	5	14	24.6
Diptera	8	1	1	4	14	24.6
Hymenoptera	1	—	1	—	2	3.5
Coleoptera	4	2	3	6	15	26.3
Others	1	6	3	2	12	21.0
Total	21	9	10	17	57	
%	36.8	15.8	17.6	29.8		100.0
Centaurea diffusa						
Lepidoptera	4	2	1	3	10	23.8
Diptera	7	—	1	3	11	26.2
Hymenoptera	1	—	1	—	2	4.8
Coleoptera	1	3	3	6	13	31.0
Others	—	4	1	1	6	14.2
Total	13	9	7	13	42	
%	31.0	21.4	16.6	31.0		100.0

[1] Agents occupying several niches are counted for each niche they occupy.

As a result of the scattered occurrence of the two knapweeds and their restricted abundance in most areas, well-developed complexes of phytophagous arthropods were seldom encountered during field surveys. The more specific agents, those species restricted to the target weeds and a few closely related *Centaurea* spp., were often absent from suitable sites within their general distribution area. For example, an analysis of the complex of root-feeding insects (12 species) at 37 localities revealed that, with the exception of *Apion* spp. (Coleoptera: Apionidae), none of the species occurred in more than a third of these localities, and that the rate of interspecific association was generally low (Müller, pers. comm.). In general, most of the host-specific arthropods were found in low number at the majority of the sites surveyed, and their occurrence over a longer period of time was quite sporadic. In these circumstances it is very difficult, if not impossible, for the survey entomologist to collect data on the impact of individual species on host plant distribution and abundance as proposed by Wapshere (1974*b*).

However, a large body of information has been collected on the time and mode of attack, as well as on the stress exerted on the attacked host plants, for most of the arthropod species closely associated with the two target knapweed species. Although no statistical analysis could be made on the impact of the arthropod community on the population dynamics of diffuse and spotted knapweed in their native range, these organisms undoubtedly exert a high consumer pressure; neither diffuse nor spotted knapweed are considered to be noxious weeds in Europe.

The Selection of Apparently Safe and Effective Biological Control Agents

It is generally recognized by biological control workers that the determination of the potential effectiveness of control agents is a very complex problem which is far from solved. Therefore the question of whether a control agent selected for host specificity screening will finally become an 'effective' control agent (i.e. will become established and affect the density and abundance of the target weed) cannot be answered in advance. However, certain guidelines have been developed during the past 20 years (e.g. Goeden 1983, Harris 1973, and Wapshere 1974*b*), which help the survey entomologist in selecting the most promising potential control agents from the complex of biotic agents encountered during field surveys. A suitable control agent should attack the target weed at an early stage or a critical time of its life cycle, for example when the plant is subjected to environmental stress. The kind of control agents needed for the successful biological control of a target weed are mainly determined by plant type (i.e. annual, biennial, or perennial), its mode of propagation and distribution, and the environment(s) where it occurs at noxious densities.

Diffuse knapweed is typically a biennial; spotted knapweed a short-lived perennial. Both species can overwinter as seeds or rosettes. Another common characteristic is their prolific seed production (up to 40 000/m^2 at high density) (Watson and Renney 1974) and their allelopathic properties (Fletcher and Renney 1963). The environmental conditions of Canadian infestations are discussed by Harris and Cranston (1979). Diffuse knapweed tends to dominate native vegetation in steppic grassland on Brown Chernozem and Brunisol in areas with an arid period in the summer. Spotted knapweed is most aggressive in the forest steppe zone on Dark Brown Chernozem. It does not compete with vigorously growing grass in moist sites nor with diffuse knapweed in steppic grassland.

To retard and possibly prevent the further spread of diffuse and spotted knapweed in North America and to reduce knapweed density in infestations, control agents feeding on flower heads and rosettes are of prime interest for biological control. Moreover, agents selected for introduction into North America have to be adapted to a steppic climate and their hibernating stages have to be able to survive the cold North American winters.

The Exploitation of Specific Food Niches by Arthropods Associated with Diffuse and Spotted Knapweed in Europe

Although the centre of the diffuse knapweed range and the eastern part of the spotted knapweed range, southern USSR, could not be surveyed, a good selection of potential biological control agents was found in the western part of the native distribution of the two knapweeds (Table 1). The exploitation of specific food niches on diffuse and spotted knapweed by specialized arthropods is shown in Table 2. The majority of species found feed on flower heads and rosettes, where they attack central buds and roots, respectively.

The general field surveys for potential control agents of diffuse and spotted knapweed and related species was terminated in 1971. By this time the life history of 12 species had been studied and the host range of 10 species had been screened. Based on the information accumulated, a list of potential control agents was established (Schroeder 1977) and updated later on (Table 3).

Table 3. List of potential biological control agents for diffuse and spotted knapweed and their host plant associations in Europe.

Agents attacking	*C. diffusa*	*C. maculosa*	*C. arenaria*	*C. vallesiaca*
Flowers and seeds				
Metzneria diffusella Englert	+	—	—	—
M. paucipunctella Zeller	—	+	—	+
Stenodes straminea (Haw.)	—	+	—	+
Urophora affinis Frfld.	+	+	—	—
U. quadrifasciata Meigen	+	+	—	—
Isolcus sp. nr. *jaceae* (Schenk.)	+	+	?	—
Shoots and leaves				
Puccinia centaureae DC.	+	+	—	—
P. jaceae Otth.	+	+	—	—
Aceria centaureae (Nal.)	+	+	—	+
Macrosiphoniella stägeri HRL.	—	+	—	+
Cassida pannonica Suff.	+	—	—	—
Phanacis centaureae (Foerst.)	+	+	—	—
Rosettes and roots				
Agapeta zoegana (L.)	—	+	+	—
Pelochrista medullana Stgr.	+	+	—	—
Stenodes meridiana Stgr.	—	—	+	—
S. straminea (Haw.)	—	+	—	+
Pterolonche inspersa Stgr.	+	+	—	—
Cheilosia sp.	—	+	—	—
Pegohylemyia centaureae Hennig	+	+	—	+
Cyphocleonus achates Fab.	+	+	—	—
Cleonus piger Scop.	+	+	—	—
Apion onopordi Kirby	+	+	—	+
A. penetrans Germar	+	+	+	—
Sphenoptera jugoslavica Ob.	+	—	—	—

The Selection of Potential Control Agents for Detailed Life-History Studies and Host Specificity Screening

Flowers and Seed-heads

In view of the prolific seed production of diffuse and spotted knapweed, the species attacking flowers and seeds were investigated first. Between 1967 and 1971, three of the six potential candidate species were studied and screened: *Urophora affinis* Frauenfeld, *U. quadrifasciata* Meigen (Diptera: Tephritidae), and *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae). They were found to be safe for release and were first released between 1970 and 1973 in British Columbia. After their establishment in British Columbia (Harris 1980*a*), releases of the two seed-head gall flies in the western United States followed between 1973 and 1980 (Maddox 1982). The flies have spread through most of the North American knapweed region, although dispersion of *U. affinis* is slower than that of *U. quadrifasciata*. Harris (1980*b*) reports a combined density related to the size of the knapweed flower head. The effect of the flies at the diffuse knapweed release site in British Columbia has resulted in a reduction of seed production from 30 000–40 000/m^2 to 1500/m^2.

M. paucipunctella attacks the seed heads of spotted but not diffuse knapweed. In British Columbia it currently attacks a third to half of the seed heads in the release stand but an average 20% of the seeds survive in attacked heads. In Europe, the moth is in fact considerably more damaging in the heads of *C. vallesiaca* which are smaller than those of the tetraploid spotted knapweed. *M. paucipunctella* coexists in the same heads with *U. quadrifasciata* but destroys the galls of *U. affinis*. Unless it can be demonstrated that *M. paucipunctella* increases the seed destruction presently achieved by the two gall flies, its distribution throughout the spotted knapweed area does not seem warranted.

In view of the impact of the combined effect of *U. affinis* and *U. quadrifasciata* on seed production of diffuse and spotted knapweed and the adaptability of the two flies to the climatic conditions in the North American knapweed area, it was decided to refrain from introducing further seed-head insects. Another two species, *Metzneria diffusella* Englert and *Isolcus* nr. *jaceae* (Schenk.) (Hymenoptera: Cynipidae), could be screened in the future if the introduction of additional species should be required. The remaining species, *Stenodes straminea* (Haw.) (Lepidoptera: Cochylidae), is no longer considered a potential control agent because it developed on a wide range of species in the tribe Cynareae, including globe artichoke and safflower, during host range screening.

Shoots and Leaves

With the exception of *Puccinia jaceae* Otth. (Pucciniaceae) and *P. centaureae* DC. (Mortensen and Harris 1983), the agents attacking shoots and leaves of diffuse and spotted knapweed have been little studied.

During 1978–80, samples of rust-infected diffuse and spotted knapweed were collected in central and eastern Europe. The material consisted of both *P. jaceae* and *P. centaureae*, but was predominantly *P. jaceae* (Watson *et al.* 1981; Watson and Alkhoury 1981). Collections from diffuse and spotted knapweed are under study at Regina and McGill University. The diffuse knapweed strain studied at Regina causes heavy infection with the attacked leaves senescing after about two weeks under laboratory conditions. The rust forms a resistant type reaction on safflower in the laboratory. Safflower is probably not damaged under field conditions and will be tested in southern France in 1984. If it can be demonstrated that safflower is not affected by the two strains of *P. jaceae* under field conditions in Europe, their release in North America can be proposed.

The leaf-gall mite *Aceria centaureae* (Nal.) (Acarina: Eriophyidae) has been observed only twice during the surveys, once in spring 1970 on *C. vallesiaca* in the Swiss Valais, and once on *C. diffusa* near Lake Skutari in southern Yugoslavia where it caused severe damage on the rosettes and shoots. The capacity of gall mites to migrate is very limited. It will therefore be difficult or impossible for *A. centaureae* to colonize scattered stands of diffuse and spotted knapweed. This may be the main reason why the mite was not found during field surveys between 1981 and 1983.

Macrosiphoniella stägeri HRL. (Homoptera: Aphididae) attacks *C. vallesiaca* and *C. maculosa* var. *rhenana*. It has been recorded from Switzerland and Germany, and also from Bulgaria and Poland where it occurs in the Pannonic steppes and other xerothermous habitats. The colonies develop on the tips of developing flowering shoots and young leaves. Heavily attacked plants die in early summer. The aphid was not found during the 1983–84 surveys, and apparently appears only occasionally in the western part of its host plant range.

Cassida pannonica Suff. (Coleoptera: Chrysomelidae) was not found during CIBC surveys; however, according to the literature it should be restricted to diffuse and spotted knapweed in the steppic region of Europe. It would seem that *C. pannonica*, like *A. centaureae* and *M. stägeri*, will only be found if the surveys can be extended to southern USSR.

Phanacis centaureae (Foerst.) (Hymenoptera: Cynipidae) forms galls in the vascular part of the stem. It is exceedingly rare in the western part of the diffuse knapweed range where it has been found only once since 1961.

Rosettes and Roots

On the assumption that the combined effect of *U. affinis* and *U. quadrifasciata* alone will not result in a general reduction in plant density of diffuse and spotted knapweed in North America, the release of agents which attack the rosettes and roots of the two knapweeds is advised. During surveys in Europe 12 species of potential interest were discovered (Table 3).

Sphenoptera jugoslavica Ob. (Coleoptera: Buprestidae), a root miner indigenous to the Balkans, was the first to be studied and screened (Zwölfer 1976). The larvae mine the central part of rosette roots of *C. diffusa* leaving a cylinder of cortex undamaged, thus are able to coexist with species that feed on the outside of knapweed roots. In Europe, attacked rosettes continue to live, but often do not flower in the following year and are subject to a second attack by *S. jugoslavica* or other root-feeding species. *S. jugoslavica* was released at two sites in British Columbia in 1976 and became established at one site (Harris and Myers 1984). The effect of *S. jugoslavica* on seed production and density of *C. diffusa* in the release site is presently being studied.

The analysis of the effect of biological control agents of diffuse and spotted knapweed in Canada has clearly indicated that additional species have to be established to reduce knapweed density below the economic threshold. Therefore, a detailed investigation of the complex of rosette- and root-feeding insects associated with diffuse and spotted knapweed and two additional *Centaurea* species, *C. arenaria* Bieb. ex Willd. and *C. vallesiaca*, was carried out by CIBC between 1979 and 1983 at 37 localities. The majority of species (with the exception of *Apion* spp.) occurred at only 40% or less of the localities studied, most likely because of the scattered host plant distribution. In addition, the rate of attack by individual species was generally low, with higher rates of attack being attained only in areas where the host plants occurred more frequently and at higher density.

Information on the occurrence of individual species in the area surveyed is now available. *S. jugoslavica* and *Pterolonche inspersa* Stgr. (Lepidoptera: Gelechiidae) are constantly associated with *C. diffusa* in Macedonia, but are absent in the eastern *C. diffusa* range, e.g. in Dobrugea, Romania, where they are replaced by *Pelochrista medullana* Stgr. (Lepidoptera: Tortricidae) and *Cyphocleonus achates* Fab. (Coleoptera: Curculionidae). These two species are widely distributed from eastern Romania westwards to eastern Austria, but are absent in the western part of the European spotted knapweed range. *Agapeta zoegana* (L.) (Lepidoptera: Cochylidae) is found throughout the spotted knapweed range surveyed, and on *C. arenaria* in eastern Romania. However, it is rare in western central Europe; e.g. the Rhine Valley. With the exception of *Apion* spp. and *Cleonus piger* Scop. (Coleoptera: Curculionidae) which apparently occur throughout the survey area, the remaining species seem to be restricted to the western and central parts of the survey area. Specifically *S. straminea* and *P. centaureae* occur more frequently and at higher density in the western part of the survey area; e.g. the Swiss Valais on *C. vallesiaca*.

During 1979 and 1981 the life history and host range of four species, *P. inspersa*, *A. zoegana*, *P. medullana*, and *S. straminea*, were studied. The Mediterranean *P. inspersa* was investigated by staff of the USDA Rome Laboratory. During host specificity screening with 49 plant species it was found that it is restricted to *C. diffusa* and accepts North American ecotypes of this species. It has been introduced into quarantine for additional host specificity screening. It is expected that *P. inspersa* will be cleared for release. In 1983 a relatively high percentage of *C. maculosa* was found attacked by *P. inspersa* in northern Hungary. This is the first CIBC record of this moth from spotted knapweed. The development of Hungarian *P. inspersa* on diffuse and spotted knapweed is presently being studied.

A. zoegana and *P. medullana* have been studied and screened simultaneously by the CIBC European Station. Both species have been cleared for release in Canada and the United States, and first releases in Canada were made in 1982 and 1983. The feeding of 1–2 larvae of *A. zoegana* destroys the roots of small rosettes, and half-grown larvae apparently actively search for additional food if a root does not sustain the complete development. This is of special interest with a view to the high plant density in North America. Moreover, multiple attack by *A. zoegana* is quite frequent, attaining 60% on *C. maculosa* and 76% on *C. arenaria*. Thus the complete destruction of big rosette roots occurs quite frequently.

P. medullana predominantly attacks *C. diffusa*, but accepts *C. maculosa* in the absence of *C. diffusa*. In contrast to *A. zoegana*, only a single larva develops on each root. Nevertheless, tests at the CIBC European Station have demonstrated that feeding of a single larva causes serious damage. Over two-thirds of well-developed rosettes were killed in late autumn prior to the hibernation of *P. medullana*. Field and laboratory observations also demonstrated that the two moths coexist without deleterious effects on either species. It is expected that the two species of cochylid moths will have an important impact on knapweed density in North America after they have become firmly established.

S. straminea has two generations a year, the autumn generation attacking the central bud and root-collar of rosettes, the summer generation the flower heads. In spite of the damage inflicted by *S. straminea* to knapweed, it had to be rejected as a biological control agent because it could develop on a wide range of species in the tribe Cynareae, including globe artichoke and safflower.

Most of the remaining seven species have no or only limited interest for biological control. *Apion* spp., although widely distributed and common, cause apparently little stress and do not affect plant growth and seed production. *Pegohylemyia centaureae* Hennig (Diptera: Anthomyiidae) is a localized species that occasionally attains high population levels on *C. vallesiaca*. Although recorded to attack diffuse and spotted knapweed, it was not found on these species during CIBC surveys. Moreover, it was not possible to breed *P. centaureae* in captivity. The same is true for *Cheilosia* sp. (Diptera: Syrphidae), which was frequently encountered in eastern Austria and Hungary in 1979 and 1980, but the populations declined since, preventing the continuation of investigations started in 1980. *Stenodes meridiana* Stgr. was found feeding on the roots of *C. arenaria* in southeastern Romania in 1980 and 1981, but was not collected in 1984. *S. meridiana* remains of interest as a potential control agent and should be studied as soon as larvae are found.

An investigation of the biology and host range of *C. achates* and *C. piger* commenced at the CIBC European Station in 1984. According to CIBC observations, the host range of *C. achates* is restricted to diffuse and spotted knapweed. Its larvae mine the roots. The shoots of attacked plants are significantly shorter than those of healthy plants and have less flowers. *C. achates* occurred with seven other root-feeding species at various localities, but coexisted only with *Apion* spp. on the same root. Interspecific competition with other root-feeding species is apparently a rare event. If it can be demonstrated that the host range of *C. achates* is restricted to knapweed, it can be considered for release in North America.

Unlike *C. achates*, *C. piger* has a wide host range and is reported to attack globe artichoke (La Ferla 1939). It is suspected that host strains exist for *C. piger*, which is common on various thistles in Europe, but which is also consistently associated with diffuse and spotted knapweed. Therefore, ovariole development, oviposition preferences, and larval survival of *C. piger* from knapweed are being studied to determine if a narrowly specific host race can be found.

Host Specificity Determination of Biological Control Agents

Screening of potential host range (host specificity) is the most crucial operation in any biological control project. Because of the overriding importance of safety, the greatest care has to be taken in selecting the appropriate test plants and in designing tests to demonstrate the safety of potential control agents beyond reasonable doubt. General considerations of this problem are found in Harris and Zwölfer (1968), Zwölfer and Harris (1971) and Wapshere (1974*a*).

The number of plants which must be included in the screening programme depends mainly on: (*a*) the taxonomic position of the target weed — whether it belongs to an isolated family or a family with close relations; (*b*) the number of closely related cultivated plants, and wild plants, which should not be attacked; (*c*) the geographic and/or ecological isolation of the release area; and (*d*) whether or not the control organism belongs to a systematic group which is known to be restricted to a small group of closely related plants (genus, subtribe, tribe) (Schroeder 1983).

Diffuse and spotted knapweed belong to the tribe Cynareae of the Compositae with a relatively large number of species, native and introduced, in the release area. Moreover, two important crops, safflower and globe artichoke, and several ornamental species cultivated in North America belong to the tribe Cynareae. This has been taken into consideration during host specificity screening of biological control agents which have been released in North America. A total of 36 plant species were screened in case of *U. affinis*, *U. quadrifasciata*, and *M. paucipunctella*, and 46 with *S. jugoslavica*. Before permission for the release of *A. zoegana* and *P. medullana* was obtained in 1982, a total of 54 plant species had to be screened, and a similar or larger number will have to be screened with *P. inspersa* and *C. achates*, and other potential control agents.

One important reason for the increased number of test plant species is the concern that insects released against knapweed might attack rare and endangered native Cynareae, especially thistles. In addition, several species of native and alien ornamental plants were tested to avoid conflicts of interest. Although the concerns of environmentalists and amateur gardeners are appreciated and seriously considered by biological control workers, the danger has to be realized that otherwise safe and effective control agents might have to be rejected in the future because of these extended safety requirements.

In view of the great economic important of diffuse and spotted knapweed to the range industry in North America, the fact that both weeds tend to dominate and suppress native flora over large areas, and danger of further spread of the weeds (Harris and Cranston 1979), the justified concerns of environmentologists and amateur gardeners have to be carefully weighed and should be subject to further discussion. It should be borne in mind that diffuse and spotted knapweed apparently cannot be controlled or even contained by chemical or mechanical means, and that biological control seems to be the sole and economically most rewarding method to resolve this important weed problem. Demands for additional test plant species should therefore be carefully assessed and only accepted after all economic and ecological aspects have been considered. It may not be possible to resolve all conflicts of interest (Andres 1981), but with improved communication between all concerned parties it should be possible to resolve most of them.

Conclusions and Recommendations

(1) As illustrated by the example of spotted knapweed, the taxonomy of a target weed may not be well known at the time when foreign exploration is being started. In such cases taxonomic studies have to be carried out in the presumed native range and the area colonized to clarify the taxonomic status of the target weed and to locate the identical taxum(a) in the native distribution area. At the same time potential biological control agents should be collected from closely related taxa (subspecies or species) and their ability to attack and develop normally on the target weed should be tested.

(2) The generally accepted guideline that foreign exploration for safe and potentially effective control agents should start at optimal survey areas (i.e. where a climatically similar region geographically overlaps the area of greatest diversification of the genus or subgenus to which the target weed belongs) could not be followed for diffuse and spotted knapweed. The best suitable survey area in southern USSR is not accessible. Surveys for biological control agents had therefore to be carried out in the marginal western range of their native distribution, in areas climatically less similar to the release areas. Nevertheless, for diffuse and spotted knapweed, the results of the field surveys justify the decision to survey marginal areas if the potentially best survey areas are not accessible.

(3) The selection of apparently safe and effective biological control agents is a difficult task for all scientists involved in foreign exploration. It is especially difficult to find such agents if field surveys have to be carried out in marginal areas of the native distribution of the target weed(s), where the plant occurs in small scattered stands and a well-developed complex of phytophagous arthropods is seldom encountered. This applied for diffuse and spotted knapweed during field surveys in central and western Europe. It has therefore not been possible to determine the impact of individual arthropod species on the distribution and abundance of the two knapweeds. However, under consideration of the biology and ecology of diffuse and spotted knapweed in North America, it has been possible to select a number of potential biological control agents by means of direct field observations and laboratory investigations in Europe.

In Europe, suitable survey areas for biological control agents of introduced North American weeds are becoming more and more rare. With a view to guarantee the further supply of control agents it may become necessary to rent and manage suitable areas in the future.

(4) The overriding importance of safety in any biological weed control operation is generally acknowledged. However, the tendency to extend the safety demands beyond

certain limits may be detrimental to biological weed control; e.g. the demand that alien control agents should not attack any rare or endangered native plant species in the release area. In case of diffuse and spotted knapweed, an otherwise safe and effective control agent may be rejected because it feeds on a rare North American *Cirsium* species (Compositae) during host specificity testing.

In view of the great economic importance of knapweed and other introduced weed species, such as leafy spurge, to the North American range industry, demands for test plant species should be carefully assessed and only accepted after all economic and ecological aspects have been considered. It would seem to be unwise and detrimental if biological weed control would be paralyzed by overstressed and/or unjustified safety demands. With improved communication between all concerned parties it should be possible to resolve most conflicts of interest associated with biological weed control.

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Seed Dispersal and the Spread of Weeds

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Abstract

Weeds colonize new habitats and maintain genetic variation between existing populations by seed dispersal. I briefly discuss current evolutionary theories regarding the selection pressures acting on plants to disperse their seeds, and how they are relevant to herbaceous weeds. Many weed seeds disperse by wind or by adhering to animal fur or feathers (burrs). Wind-dispersed seeds from low-growing weeds often do not travel long distances, mainly because their low height of release does not allow them to be airborne for long periods of time. By contrast, burrs can adhere to and be carried by their dispersal agents indefinitely, and so have the potential to travel very long distances. More herbaceous weed species are wind-dispersed than burr-dispersed despite the longer dispersal distance achieved by burrs. I suggest that this is because wind is a more reliable dispersal agent in the relatively open habitats where herbaceous weeds occur.

La Dispersion des Graines et la Propagation des Mauvaises Herbes

C'est au moyen de dispersion de graines que les mauvaises herbes colonisent des habitats nouveaux et qu'ells maintiennent la variation génétique entre leurs populations actuelles. Je passe en revue brièvement les théories d'évolution admises à propos des pressions sélectionelles qui amènent des herbes à disperser leurs graines, ainsi que la manière dont ces thérories s'appliquent aux mauvaises herbes. Beaucoup de graines de mauvaises herbes se dispersent au moyen du vent ou en s'attachant au pelage ou aux plumes d'animaux. Fréquemment, les graines de mauvaises herbes ne traversent que des distances courtes, parce que la petite hauteur à laquelle elles sont lâchées ne leur permet pas de se faire transportés longtemps par le vent. Par contre, les capsules épineuses, qui peuvent s'attacher indéfiniment aux agents de dispersion, ont le pouvoir de traverser de longues distances. Plus d'espèces de mauvaises herbes doivent leur dispersion au vent, qu'aux capsules épineuses, malgré la superiorité de celles-ci comme voyageurs. Je considère qu cela resulte de la plus grande sûreté du vent comme agent de dispersion dans les habitats relativement ouverts, où se trouvent les mauvaises herbes.

Introduction

Seed dispersal is the means by which plants colonize new habitats: the spread of weeds is contingent on widespread seed dispersal and the ability of seedlings to establish and reproduce in a variety of environmental conditions (Salisbury 1961). (For convenience, all plant propagules will be referred to as 'seeds', even though they may technically be achenes, nutlets, etc.) The influx and establishment of seeds into new habitats has consequences for weed control. Firstly, seed dispersal may promote the introduction of exotic species into geographic regions where their limiting agents do not exist (Room 1981). In addition, seed dispersal promotes gene flow and introduces and maintains genetic variation between and within plant populations. This is relevant to weed control because asexual, uniform populations are thought to be easier to control than genetically diverse populations (Burdon *et al.* 1981). Likewise, the input of small numbers of seeds ('founder populations') into new habitats may result in populations with low genetic variation (especially if plants reproduce asexually) and these may be somewhat easier to control (Harper 1977).

The evolutionary factors selecting for dispersal of seeds away from the parent plant are discussed in detail in Howe and Smallwood (1982). Three selection factors have been hypothesized as acting on seed dispersal: (1) escape from the parent plant; (2) colonization of new habitats; and (3) 'directed', or non-random dispersal of seeds to favorable habitats.

These hypotheses are not mutually exclusive. The first two hypotheses concern dispersal distance. The 'escape' hypothesis postulates that mortality due to seed predation, fungal pathogens, and sibling competition is greater below the parent plant than anywhere else, so that long-distance dispersal away from the parent plant is favored (Augsberger 1983). This hypothesis generally applies to plants growing in stable habitats. The 'colonization' hypothesis applies to plants occupying the early stages of succession. These early colonizers produce an environment where other plant species become competitively superior, and the original plants are then under strong selection pressure to disperse seeds to new, unoccupied habitats (Horn 1974). 'Directed' dispersal concerns plants occupying habitats with special edaphic conditions, so that non-random dispersal to habitats with the same conditions is more important to fitness than dispersal distance. 'Directed' dispersal is probably not relevant to weeds, which are characterized by their wide tolerance of environmental conditions.

A fourth type of dispersal that is common in weedy plants is dispersal through 'time'. Seeds that disperse through time do not possess morphological adaptations for long distance dispersal (pappus, barbs, fleshy fruits), but are viable in the soil for long periods of time (50 years is not uncommon; Werner 1979). The habitats occupied by species that disperse through time are usually inhospitable to prolonged adult survival, often because they are continually disturbed (Werner 1979). 'Dispersal' occurs when seeds germinate and establish in the sites previously occupied by their parents.

This paper deals principally with long-distance dispersal since it is the means by which weeds spread and colonize new habitats. First, I review the major mechanisms by which seeds of herbaceous weedy plants disperse away from the parent plant. Second, I discuss differences in the dispersal distance achieved by wind and adhesively dispersed seeds. I briefly describe some experimental results showing how the morphological characteristics of burrs influence dispersal distance. Finally, I put forward some hypotheses to explain why selection has favored wind over adhesive dispersal in many weed species. The mechanisms discussed (and arguments developed) in this paper are restricted to terrestrial weeds of short (1.5 m or less) stature.

Seed Dispersal Mechanisms of Weeds

Weeds are often spread to new continents by human activities (Salisbury 1961; J.H. Myers, pers. comm.). Most herbaceous weed seeds that disperse to new habitats are transported by wind (308/544 species of 'weedy' Compositae) and adhesively on animal fur or feathers (57/544 species of 'weedy' Compositae). (The remainder of the 544 species are dispersed through 'time' or using scales that function in orientation during dispersal and on the ground; data from a pan-global survey of 18 regional floras by Venable and Levin (1983). See Werner (1979), and Howe and Smallwood (1982) for data on dispersal mechanisms of other plant families.) Relatively few herbaceous plants disperse their seeds as fleshy fruits; this dispersal mode is mostly restricted to woody plants (Levin and Kerster 1974; Sorensen 1981, 1984). Seeds that possess morphological adaptations for long-distance dispersal do not usually remain viable in the soil for long periods of time, and many plants which produce seeds with morphological adaptations for dispersal are also able to reproduce vegetatively by cloning (Werner 1979; Venable and Lawlor 1983). It has been hypothesized that dispersal is at a premium in perennials because there are few sites for recruitment near the parent plant (Cook 1979; Werner 1979).

The distance travelled by wind-dispersed seeds is principally determined by the height of seed release, the speed that the seed falls through the air (terminal velocity), the speed and turbulence of the wind between the ground and the point of release, and the presence of obstructions in the seed's path (Harper 1977). Wind-dispersed seeds from plants of short stature (i.e. herbaceous weeds) growing in dense stands usually travel short distances because of their low height of release and the presence of obstructions (Harper 1977). Even when obstructions are not present (i.e. the habitat is not densely vegetated), the distance travelled by wind-dispersed seeds of short herbaceous plants is often not more than a few metres (Harper 1977; Waser *et al.* 1982; but see Platt 1975 for examples of wind-borne seeds that can travel several hundred metres).

Adhesively dispersed seeds (burrs) have the potential to be transported much longer distances than wind-dispersed seeds because they can be carried indefinitely on animal fur or feathers. Adhesive seeds may remain on animals until the animal molts or dies (Agnew and Flux 1970). Burrs may travel shorter distances if they passively drop off, or they are detected and removed by the animal shortly after attachment. However, even a short retention time may result in relatively long-distance dispersal if the host animal travels at a good speed.

Burr Morphology and Dispersal Distance

The potential for long distance seed dispersal may make the spread of burr-bearing weeds particularly difficult to control. The pan-global occurrence of several species of economically important weeds must be attributed, at least in part, to long distance seed dispersal of their burrs. Three cosmopolitan weeds, *Xanthium* spp. (Compositae; cocklebur, noogoora burr), *Arctium* spp. (Compositae; burdock), and *Tribulus* spp. (Zygophyllaceae; puncture vine) are dispersed as burrs. The burrs of *Xanthium* and *Arctium* seriously decrease the value of wool (Gross *et al.* 1980; Weaver and Lechowicz 1982), and *Tribulus* burrs cause stress to livestock and may puncture the stomach linings of the animals that consume them (Sankaran and Ramaseshiah 1981). In addition, forage of *Arctium* and *Tribulus* is poisonous to livestock and all three species compete with crop plants (Gross *et al.* 1980; Sankaran and Ramseshiah 1981).

The burr morphology of *Arctium* spp. and *Xanthium* spp. varies greatly within species, populations, and individual plants (Hawthorn and Hayne 1978; Hare and Futuyma 1978). I hypothesize that this variation in burr size and morphology has an important influence on seed dispersal distance. I predict that burrs of certain sizes and shapes are very irritating to animals, and that these burrs will be removed shortly after attachment. I tested the following hypotheses using burdock (*A. minus* [Mill.] Bernh.) burrs and captive snowshoe hares (*Lepus americanus* Erxleben) (Lagomorpha: Leporidae): (1) Small burrs are less irritating to animals than large burrs, and so should be retained for longer periods of time than large burrs; (2) Burrs attached to the pads of animal's feet are more noticeable than burrs attached to other body areas (e.g. the back). Back burrs should therefore be retained longer (and travel farther) than feet burrs; and (3) Burrs attached to an animal in low numbers (e.g. 2 burrs/hare) are less irritating to animals than burrs attached in high numbers (e.g. 16 burrs/hare), and so should be removed less quickly. That is, the mean retention time of a burr should be longer for burrs attached in low numbers than burrs attached in high numbers.

From the plant's perspective, the first hypothesis refers to whether selection for long-distance dispersal has favored the production of burrs of a certain size. The second hypothesis refers to whether a plant drops its burrs to the ground (where they would attach to an animal's feet), and the height of burrs in relation to where they attach to an animal. The third hypothesis refers to the numbers of burrs that detach from the plant during an encounter with an animal.

The experiment testing these hypotheses involved applying *A. minus* burrs of different sizes and numbers to different body positions of four captive snowshoe hares. The experimental results confirmed all three hypotheses: (1) small burrs were retained longer than large burrs; (2) burrs on the back were retained longer than burrs on the feet; and (3) burrs attached to hares in low numbers had longer mean retention times than burrs attached in high numbers. All these results were statistically significant (Sorensen, in prep.). Moreover, it was not uncommon for the burrs to be retained for up to 24 h, which could result in dispersal to long distances. The relationship between burr characteristics, retention time, and dispersal distance in the field will also be determined by the distance travelled by the animal in its home range, and whether burrs are knocked off the animal by chance.

The relationship between burr size, burr number, dispersal agent body position ('feet' *vs.* 'back') and retention time has implications for the evolution of burr and plant characteristics. Since burr size and seed number are positively correlated in *A. minus* (burr weight and seed no., $r = .839$, $N = 50$; burr length + width and seed no., $r = .768$, $N = 50$), small burrs may go longer distances than large burrs, but fewer seeds are dispersed/burr. Likewise, burrs attached in low numbers may be retained on animals for long periods of time, but fewer seeds are dispersed than when burrs are attached in high numbers. Finally, with regard to the longer retention time of 'back' burrs compared to 'feet' burrs, it may be relevant that *A. minus* plants drop relatively few of their burrs to the ground (approximately 20% dropped, Hawthorn and Hayne 1978). Another species of *Arctium*, *A. lappa*, drops up to 60% of its burrs (Hawthorn and Hayne 1978). Many of the 'dropped' *A. lappa* burrs may be taken to new locations by the wind, but some must stick to the feet of animals. *A. lappa* plants probably disperse more burrs than *A. minus* plants (which may have low burr removal rates; Hawthorn and Hayne 1978), but the *A. minus* burrs that do attach to dispersal agents may travel longer distances. Future research will test these generalizations by examining the distance travelled by marked burrs.

Adhesive *vs.* Wind Dispersal

I have argued that many weedy plant species are under strong selection pressure to disperse their seeds to new habitats. I have also argued that adhesive seeds have the potential to disperse to much greater distances than wind-dispersed seeds. These arguments appear to contradict the evidence: in general more 'weedy' plant species are dispersed by wind than by adhesion (Werner 1979; Venable and Levin 1983). I hypothesize that there is strong selection against adhesively dispersed seeds because their encounter rates with dispersal agents may often be low. For example, there is evidence that individual plants of *A. minus* and *Daucus carota* L. (Umbelliferae) have very few of their burrs removed by animals (Hawthorne and Hayne 1978; Lacey 1981) during a season. Selection may favor wind-dispersal in habitats where plants are under strong selection pressure to disperse seeds away from the parental site because wind is a more reliable (albeit less effective) dispersal agent. By contrast, most of the relatively open (disturbed and cultivated) habitats where weeds occur almost always receive some wind, but visits by animals may be infrequent. (Burrs may be more common than wind-dispersed seeds in closed habitats which receive almost no wind, such as the forest floor; Stebbins 1974.) Future work will involve testing these hypotheses by examining the removal rates and distances travelled by wind and adhesively dispersed seeds in the field.

Some weed species exploit both wind and adhesive dispersal agents by producing heteromorphic seeds. Two composite species (*Picris echioides* L. and *Hypochoeris glabra* L.) produce dimorphic seeds where one morph is wind-dispersed and the other morph is adhesively dispersed (Sorensen 1978; Baker and O'Dowd 1982). In both species, the adhesively dispersed seeds occur on the periphery of the capitulum and are slightly larger than the wind-dispersed seeds. The morphs do not differ in germination or competitive ability, and the main difference between them appears to be dispersal. The ratio of animal to wind-dispersed seeds of *H. glabra* varies according to plant density: high ratios of adhesive to wind-dispersed fruits are produced when plants grow in dense stands. This is thought to be advantageous to *H. glabra* plants because obstructions by neighbouring plants reduce the efficiency of wind-dispersal (Baker and O'Dowd 1982). The production of heteromorphic seeds ensures transport away from the parent plant even if only one dispersal agent is available. In addition, successful seed transport by both agents promotes the dispersal of seeds to a variety of distances and habitats. The spread of *P. echioides* and *H. glabra* may be limited only by the ability of seeds to establish and reproduce in the sites where they land.

Conclusions

Seed dispersal is responsible for the spread of weeds into new habitats and also for maintaining genetic variation within pre-existing weed populations. Both these factors have implications for weed control.

Many weed seeds are dispersed away from the parent plant by wind or by adhesion to animal fur or feathers (burrs). Burrs have the potential to travel farther than wind-dispersed seeds because they can be carried on animals for very long periods of time. Experimental results suggest that the morphological characteristics of burrs affect how long they remain on an animal before they are groomed off. This finding has implications for the evolution of plant characteristics, and may provide important clues on how weeds spread.

Despite the potential of burrs to disperse to proportionately longer distances, more species of weedy plants are dispersed by wind. I hypothesize that this is because wind is a more reliable dispersal agent in the open, disturbed areas where weeds occur. This hypothesis needs to be tested by monitoring seed removal rates of weeds producing wind- and adhesively-dispersed seeds in a range of habitats. The relationship between plant characteristics, seed dispersal, and the spread of weeds clearly deserves further work.

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Climatic Influences on Weeds and their Herbivores: Biological Control of St. John's Wort in British Columbia

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Abstract

The biological control of St. John's wort (*Hypericum perforatum*) in British Columbia is an example of climatic limitations of successful weed control. In some areas of British Columbia complete control of St. John's wort has not been achieved despite the presence of an apparent abundance of the biological control agents, chrysomelid beetles. Areas of successful control have climates similar to the native Mediterranean habitat of *Chrysolina quadrigemina*, characterized by warm, dry summers. Areas where the weed persists in large stands have moister, colder weather, and the dominant beetle species is *C. hyperici*. Results of field and laboratory studies were used to demonstrate ways in which temperature may determine beetle species composition, reproduction, and feeding activity. Greenhouse and field studies demonstrate the beneficial effect of moisture on St. John's wort seed germination and recovery from herbivory.

Effets du Climat sur les Plantes Nuisibles et les Herbivores: Lutte Biologique Contre le Millepertuis Perforé

Si le climat peut gravement perturber la reproduction et l'alimentation des insectes utilisés comme agents biologiques, lemauvais temps peut aussi nuire à la croissance des plantes et à leur capacité de récupération après les attaques des herbivores et limiter leur aire de propagation. La théorie relative à la lutte biologique reconnaît généralement l'importance du climat pour le succès de l'établissement des insectes, mais les effets du temps sur les mauvaises herbes peuvent aussi influer sur la lutte biologique. La lutte biologique contre le millepertuis perforé en Colombie-Britannique est un exemple des contraintes imposées par le climat à l'élimination des plantes nuisibles. Dans certaines régions de la Colombie-Britannique, les millepertuis perforés n'ont pas été entièrement éliminés en dépit de l'abondance apparente des coléoptères. La lutte a été efficace dans les régions dont le climat est similaire à celui de l'habitat de *Chrysolina quadrigemina*, espèce originaire des zones méditerranéennes où les étés sont chauds et secs. De vastes touffes de plantes nuisibles persistent dans les régions humides et plus froides, où l'espèce dominante est *C. hyperici*. Les résultats des études sur le terrain et en laboratoire ont servi à montrer comment la température peut influer sur la composition, la reproduction et l'alimentation des espèces de coléoptères. Les études en serre et sur le terrain mettent en évidence les effets de l'humidité sur la capacité de récupération du millepertuis perforé attaqué par les herbivores et sur sa reproduction.

Introduction

While climate may severely constrain insect control agent reproduction and feeding activity, poor weather may also reduce plants' capacities to grow and recover from herbivory, and may limit propagation. Biological control theory traditionally recognizes the importance of climate for the successful establishment of insects (DeBach 1964), but the weather's effect on weeds may also influence biocontrol (see references in Harris 1980).

For example, variations in the density of the weed, tansy ragwort (*Senecio jacobaea* L.; Compositae) can be related to climatic factors (Dempster and Lakhani 1979). In a study of the relationship of tansy ragwort and the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), Cox and McEvoy (1983) demonstrated that moisture availability can limit plant compensatory growth after defoliation.

The noxious range weed, St. John's wort, *Hypericum perforatum* L. (Clusiaceae), has been limited to economically acceptable levels over millions of acres in North America (DeBach 1964). However, it remains a problem in parts of Canada, United States, and Australia where summer rainfall is common (Delfosse and Cullen 1981; Harris and Maw 1984), even though some of those areas experience periodic defoliation by chrysomelid beetles (Delfosse and Cullen 1981; Williams, Myers, and Edwards, unpubl. data). We have examined the system of *Hypericum* and the chrysomelid beetles introduced as control agents in diverse habitats of British Columbia to examine the influence of temperature and rainfall on populations of weeds and their control agents.

Table 1. Habitat differences of the Okanagan and East Kootenay Valleys of British Columbia (means ± s.e.).

Parameter	Okanagan	E. Kootenay
Temperature (°C)	Mean max./mean min.	Mean max./mean min.
Sept.–Feb. (fall–winter)	7.5 ± 1.2/–1.0 ± 0.8	4.9 ± 1.3/–5.1 ± 1.0
Mar.–Aug. (spring–summer)	19.0 ± 1.0/6.6 ± 0.8	17.7 ± 1.1/4.2 ± 0.8
Rainfall (mm)		
Sept.–Feb.	121.8 ± 19.1	184.4 ± 33.1
Mar.–Aug.	146.9 ± 15.5	322.8 ±5.8
Snowfall (cm/yr)	79.5 ± 15.1	167.4 ± 16.9
Soil type	Fertile alluvial	Glacial gravel
St. John's wort phenology	Plants senesce during summer	Many remain green during summer
Control	Complete	Ineffective

Unsuccessful weed control in new habitats may be a result of: (1) inadequate herbivore performance; or (2) superior performance of the plant under the new environmental conditions. In the case of persistant St. John's wort in the East Kootenay of British Columbia, the beetles appear to have established populations and consume considerable amounts of the weed (in some springs they consume almost all of the spring rosette growth, Williams, Myers, and Edwards, unpubl. data). Therefore, the purpose of this study was to examine the hypothesis that weather in the E. Kootenay might improve St. John's wort growth and reproduction.

Materials and Methods

Study Sites

Chrysolina quadrigemina (Suffr.) and *C. hyperici* (Forst.) (Coleoptera: Chrysomelidae) successfully controlled outbreaks of St. John's wort in California and Australia and were introduced to control the weed in British Columbia in the 1950s (DeBach 1964). The weed occurs across the Province from Vancouver to the E. Kootenay Valley of southeastern B.C. In the mid-1900s St. John's wort presented a serious problem in the Okanagan and Kettle Valley rangelands of southern B.C. (DeBach 1964). Although it took 7–10 years for the beetle populations to become established, the weed was reduced to acceptable levels in many parts of B.C. Two areas were chosen for study: the Okanagan Valley as a site of successful control, and the E. Kootenay Valley as a site of ineffective control. The E. Kootenay and Okanagan habitats differ considerably in temperature, precipitation, and soil types (Table 1), and in the E. Kootenay the beetles have established populations but the weed persists in relatively pure stands (Harris and Maw 1984; Williams, Myers, and Edwards, unpubl. data).

Seed Germination

To examine the effect of rainfall patterns on seed germination of St. John's wort, seeds were collected from plants around Vancouver (on the University of British Columbia campus) in June 1984. Seeds from several plants were combined to control for interplant variations. Fifteen plastic petri dishes (1.5 cm deep) were filled with potting soil and 200 seeds/dish were planted just below the soil surface. Five dishes each were used in three treatments: (1) WET — soil kept constantly moist; (2) WET ONCE – soil watered once, initially, then allowed to dry; and (3) DRY — soil remained dry. Petri dish lids were replaced and the dishes were kept in a controlled temperature chamber at 20°C, 10 hr daylength, to mimic field conditions for germination. The dishes were checked daily until the first cotyledons showed above the soil. New seedlings were counted periodically thereafter (Table 2) and all seedlings were removed after they were counted.

Table 2. Germination of St. John's wort (*Hypericum perforatum* L.) seeds under several moisture conditions. Numbers represent mean cumulative numbers of seeds (± s.e.) germinating in three treatments (with five replicates of 200 seeds each).

Day of Experiment	Treatment		
	Wet	Wet Once	Dry
7	32.0 ± 4.1[1]	0[2]	0[2]
14	47.0 ± 5.9	0	0
16	59.8 ± 8.6	0	0
18	73.4 ± 9.8	2.2 ± 1.0[1]	0
21	—	—	0[1]
25	83.8 ± 11.1	5.2 ± 0.9	1.4 ± 1.4
30	87.0 ± 9.5	5.8 ± 0.8	2.2 ± 1.5

[1] Begin experimental protocol: soil kept wet.

[2] Begin experimental protocol: soil allowed to dry between waterings.

Defoliation Experiment

A field experiment was conducted to determine the effect of herbivory on young shoot growth of St. John's wort. Seventy St. John's wort (mean shoot length = 45.1 ± 2.9 cm) were transplanted into the U.B.C. field laboratory on campus from an undeveloped area about 2 km away. The plants were watered regularly and allowed to establish for 3 wks after transplantation. At that time, all of the plants were completely defoliated (all green shoots were removed). Thirty-five of the plants were designated as the experimental group. Biweekly for the next 6 wks, shoot length/plant was measured and the experimental plants were defoliated again. The mean total shoot length produced/plant during the experiment for the treatment and control groups was compared using a t-test.

Field Studies

Observations were made and data collected at the Okanagan and E. Kootenay study sites in 1981, 1982, and 1983 (Williams, Myers, and Edwards, unpubl. data). Temperature and precipitation information used in this study was collected by Environment Canada at weather stations at the Kelowna Pollution Control Center (near the Okanagan site) and at Elko (near the E. Kootenay site).

Results

Rainfall

In the E. Kootenay during the summer months, rainfall occurs more regularly and in greater amounts than in the Okanagan (Table 2). Thus, because of its lower summer rainfall, the Okanagan climate resembles a classic Mediterranean habitat more closely than that of the E. Kootenay. That resemblance to the native climate of St. John's wort is also reflected in the summer senescence of St. John's wort in the Okanagan (Edwards 1982).

Table 3. Monthly mean precipitation (mm ± s.e.) in British Columbia. Data were compiled from 1975–81.

Month	Okanagan	E. Kootenay
Apr.	25.7 ± 7.3	123.1 ± 52.2
May	32.2 ± 4.8	73.0 ± 10.4
June	26.7 ± 3.3	77.2 ± 10.0
July	19.0 ± 2.5	63.7 ± 14.8
Aug.	40.3 ± 8.4	61.7 ± 12.0
Sept.	21.4 ± 7.8	31.6 ± 5.2

Seed Germination

When exposed to continually wet conditions, 16±2% of the seeds germinated after 7 d. When seeds in the WET ONCE treatment failed to germinate after 7 d, the protocol was altered to wetting the soil shortly after it dried out (about 3-day intervals). No seeds had germinated after 7 d more, so the soil was watered and kept moist to determine seed survival. Four days later (day 18 of the experiment) cotyledons appeared, but comparing the numbers of seedlings appearing after watering in the WET ONCE and the WET treatment, mortality in the former appeared to have been high (Table 3). No seeds germinated in the DRY treatment after 7 d either, and the protocol for them was shifted to 'wet when dry' (as described above). No seeds had germinated after 14 d more, and the soil was watered and kept moist to determine the relative seed survival. Four days later, seeds began to germinate (on day 25 of the experiment), and after 30 d mortality in that treatment appeared to be even greater than in the other treatments. In summary, St. John's wort seeds seem to require 7 d of continuous moisture, or slightly less after periodic watering. Periodic watering appeared to decrease survival, perhaps due to desiccation of very young seedlings.

Defoliation Experiment

The total shoot length produced by plants that were defoliated once only and by plants defoliated repeatedly was not significantly different. The 'control' plants produced

31.4±3.7 cm and the 'defoliated' plants produced 25.0±3.7 cm new growth ($t = 1.21$, $P>0.1$). An unexpectedly heavy amount of rain fell on Vancouver during the time of the experiment. In fact, rainfall on the U.B.C. field site during the experiment was within the range of rain that falls on the E. Kootenay at the same time of year (77.5 mm at U.B.C. *vs.* 63.7±14.8 mm at Elko, 1975–81). Thus, the result that compensatory growth of shoots after defoliation was equivalent to shoot growth of control plants suggests that the relatively abundant rainfall of the E. Kootenay may allow equally robust recovery from herbivory.

Discussion

The moist summer climate of the E. Kootenay appears to permit greater reproductive output of St. John's wort by enhancing germination, and may improve the ability of plants to recover from herbivory. In their native habitats *C. quadrigemina* and *C. hyperici* feed and reproduce in fall, winter, and spring. In Mediterranean climates the winter and early spring defoliation by adults and larvae is followed by the annual summer drought and has been regarded as crucial to successful St. John's wort control (Clark and Clark 1952). However, the severe winter weather of B.C. constrains beetle activity and temporally limits herbivore pressure on the weed populations.

In California and Australia, *C. quadrigemina* begin to mate and oviposit soon after they emerge from aestivation in early autumn. In contrast, mating and oviposition by *C. hyperici* in the autumn is delayed by as much as 4 months (Holloway and Huffaker 1951; Clark 1953; Harris 1962). The phenological difference between the species limits *C. hyperici* exposure to harsh autumn and winter temperatures and appears to confer a substantial advantage to *C. hyperici* in terms of survival and reproductive output (Williams, unpubl. data). In this system, as in any other, selection acts to improve the survival of individuals. The apparent selective advantage of *C. hyperici* in the E. Kootenay seems to be manifested in the beetle species composition there, where *C. hyperici* predominates (75% of the beetles in spring). While the delayed activity of *C. hyperici* improves their survival, the relatively short period of feeding limits the herbivore pressure on St. John's wort and, thus, reduces the level of biological control achieved.

Several studies have examined herbivory and discussed how insect predation on seeds (Louda 1982) and plant parts (see references in Derizo 1984) may limit plant populations. However, the influence of weather on the interactions of herbivores and their host plants, and successful control of weeds, such as St. John's wort and tansy ragwort (Myers 1980; Cox and McEvoy 1983), is crucial. In eastern B.C., and perhaps other moist areas, the St. John's wort plants appear to have an ecological advantage over their herbivores, due to their ability to tolerate habitat differences. I propose that the successful control of St. John's wort by *Chrysolina* around the world has resulted, in large part, from the herbivore acting in concert with summer water stress characteristic of a Mediterranean climate. When that stress is relieved, as it is in eastern B.C., herbivory by *Chrysolina* is not sufficient to limit St. John's wort populations. In such systems, biological control may be improved by augmenting the pressures on the plant imposed by other control agents, or with improved competition by native plants (Harris 1980).

In conclusion, the impact of herbivory on plant population dynamics must be evaluated in the context of other features of the plants' environment in order to improve the predictability of the outcomes of biological control strategies.

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Chapter Two
Economics of Biological Control of Weeds

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Factors Affecting the Economic Feasibility of the Biological Control of Weeds

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Abstract

Studies examining the economics of biological control of weeds have focused on conceptualization of the broad, societal benefits that justify public expenditure on biocontrol research and implementation. Consideration of the acceptability and desirability of biological control from the perspective of its users consequently has been overlooked. However, it is the support of eventual users of a biocontrol technique that ultimately determines success. Assessment of economic feasibility, the capability of a biocontrol technique to yield equivalent or greater net returns to users than do current weed control practices, is an important first step in evaluating and selecting approaches for research or implementation. Economic feasibility is greatest for situations under which: (a) target weed damage is perceived by potential biocontrol users as an economic problem; (b) the target weed is a singly-occurring major weed problem on high-valued land but causes low to moderate damages per weed individual; (c) current methods for control of the target weed are either unavailable, or their direct and indirect costs are high; (d) the biocontrol agent is technically effective; (e) the effect of the agent on the weed is rapid and reliable; (f) users' direct and opportunity costs of employing the biocontrol tactic are low; and (g) the interrelationship of these characteristics results in higher net returns to the use of biological control than available nonbiological alternatives. Once economic feasibility has been verified, the biocontrol targeting process can further be refined by examining the commercial potential and/or broader societal impacts of economically feasible tactics' implementation.

Facteurs Influant sur la Faisabilité Économique de la Lutte Biologique Contre les Plantes Nuisibles

Les études portant sur les aspects économiques de la lutte biologique contre les plantes nuisibles se sont concentrées sur la conceptualisation des avantages d'ensemble pour la société justifiant les dépenses publiques en recherche et en application de la lutte biologique. On n'a donc pas tenu compte des aspects d'acceptabilité et de désirabilité de la lutte biologique du point de vue des utilisateurs. Cependant, c'est l'appui des utilisateurs éventuels d'une technique de lutte biologique qui détermine en fin de compte son succès. L'évaluation de la faisabilité économique, la capacité d'une technique de lutte biologique à permettre aux utilisateurs de réaliser des bénéfices équivalents ou supérieurs à ceux permis par les pratiques courantes de lutte coutre les plantes nuisibles, constitue une première étape important dans l'évaluation et le choix des méthodes de recherche et d'application. La faisabilité économique est particulièrement nécessaire dans les cas où (a) les utilisateurs éventuels de la lutte biologique considèrent les dommages causés par la plante nuisible cible comme un problème économique; (b) la plante nuisible visée constitue le seul problème important de plantes nuisibles sur les terres à valeur élevée, mais ne cause que des dommages faibles à modérés par plant individuel; (c) les méthodes courantes de lutte contre la plante nuisible visée sont inaccessibles ou leurs coûts directs et indirects sont élevés; (d) l'agent de lutte biologique est techniquement efficace; (e) l'effet de l'agent sur la plante nuisible est rapide et fiable; (f) les coûts directs et occasionnels des utilisateurs reliés à l'emploi de la méthode de lutte biologique sont faibles; et (g) la corrélation de ces caractéristiques se traduit par des bénéfices plus élevés avec la lutte biologique qu'avec les méthodes de lutte non biologiques disponibles. Une fois la faisabilité économique vérifiée, on peut continuer d'affiner le ciblage de la lutte biologique en examinant les possibilités commerciales et les effets d'ensemble sur la société de l'application des méthodes économiquement faisables.

Introduction

During a time when agricultural research funding is limited, competition among areas of investigation is fierce, and matriculation of agricultural scientists is ebbing, it is especially important to focus applied research on techniques that have a high probability of successful implementation. Assessment of the potential economic feasibility of technological possibilities is a valuable input to the research decisionmaking process. Consideration of factors affecting economic feasibility of biological control of weeds can help guide research efforts towards those techniques most likely to successfully demonstrate the potential for biological control of weeds.

The economic performance of biological control technology is determined by the interactions among the populations of at least three species — the biological control agent; the pest organism; and the human population whose activities are disrupted by presence of the pest. In agricultural systems, man's activities involve additional species — the crop or livestock populations affected by the pest. But these commercial species are important only in terms of how they contribute to the achievement of man's objectives.

While much has been written about the conceptual aspects of evaluating biological control of weeds (Andres 1977; Harris 1980; Tisdell *et al.* 1984), little work actually has been done to accurately quantify the benefits and/or cost of weed biocontrol. What economic accounting has been achieved (e.g. Cullen 1978; Harris 1979) focuses on biological control research project benefits and costs. Measurement of net expected economic returns to the primary beneficiaries (users) of the biocontrol technique, a critical clue to the probable success of the technology itself, tends to be ignored or is so deeply imbedded in a broader attempt at project justification that it is inextricable for research decisionmaking purposes.

This paper explains how information obtained from user-oriented economic feasibility studies differs from the results of project justification efforts, why assessments of economic feasibility are independently valuable in selecting weed and biocontrol agent subjects for study, and what is required to examine the economic feasibility of biological control possibilities.

The Concept of Economic Feasibility

Economic feasibility here refers to the capability of a given biological control technique to yield equivalent or greater net returns to its user as do current weed control practices. The concept is user-oriented. The user is the farmer, rancher, irrigation commissioner, etc., who directly experiences the weed problem. Net returns are the benefits obtained by the user from weed control, minus the costs the user faces to achieve control. The nature of these benefits and costs is determined by the objectives of the user. In the case of users whose objective is to maximize profit obtained from an economic enterprise (such as crop production), costs and benefits are fairly straightforward and measured in monetary terms. Users whose objective is to minimize risk (as in the case of subsistence farmers requiring a minimum level of food production to avert disaster) view benefits and costs differently. This group attaches a higher than strictly monetary cost to techniques that have even minimal risk of failure. Users facing a fixed budget may be more concerned with cost minimization, an objective through which benefits of a technique are discounted as cost of the technique approaches or exceeds a maximum amount.

The importance of the economic feasibility concept is that users who cannot expect to gain, by whatever criteria, from the use of a particular weed control technique, have little or no incentive to adopt or utilize, or preserve the potentially broader benefits of the technique. Thus, success of any given biological control alternative is ultimately judged by the economic feasibility of its implementation.

The concept of economic feasibility is narrow to the extent that it does not incorporate the entire range of benefits and costs to society. However, for two important reasons, assessment of economic feasibility is a logical first step in judging overall implications of alternative methods for biological control of weeds. First, if a biological control technique is not economically feasible from the perspective of its target user group, there is no need to estimate broader economic implications of the technique because it will not be adopted (unless the user is subsidized). Full accounting of the total environmental, market, and other social costs of a biocontrol approach involves considerable effort. This effort is neither necessary nor justifiable unless the technique's basic economic feasibility is first established. By making feasibility assessment a first step in evaluation and comparison of alternative techniques, unnecessary work can be avoided.

Secondly, information needed to estimate economic feasibility is a prerequisite for examining the full economic implications of a technique's implementation. Benefit/cost analysis incorporates both private and public gains and losses, and determines whether research and development or implementation of a technique is justifiable when total societal economic returns are considered. Economic feasibility assessment provides the measures of private benefits and costs that are components of a benefit/cost analysis.

Factors Affecting Economic Feasibility

A range of biotic, abiotic, social, and economic factors interact to determine the comparative economic advantage or disadvantage of biological control (Reichelderfer 1981). In the following discussion, the independent effects of those factors most critical to the economic feasibility of the biological control of weeds are reviewed.

Impact of Target Weed on Economic Activity

By definition, a weed is a plant out of place. But, the effect of this displacement in an economic system can range from insignificant to devastating. A number of different relationships determine the extent of impact. In selecting the best set of weeds for biocontrol research, each of the following components must be examined.

Weed status. In what way does the weed interfere with man's activities? What value does the affected group place on this interference? These are two of the questions to be addressed in examining the status of a given weed in an economic system. The first is primarily a function of losses — such things as reduction in crop yield, product contamination, reduced weight-gain or fertility, poisoning of livestock, decreased water flow, or decline in land value. While estimation of physical losses is essential, it is equally important at early stages in the consideration of various weeds as biocontrol targets, to determine how the group affected by the weeds perceives the issue of loss. Weed severity needs to be based on sociological, psychological, and economic criteria distinct from purely physical damage relationships. Bypassing an assessment of the potential biocontrol user group's perception of the weed can lead to erroneous assumptions regarding the weed's status. For example, Hilldebrand (1981) reports the case of Guatemalan farmers who rejected recommendations for control of weeds that limit vegetable yield. The reason for rejection was that the farmers used the 'weed' species as a supplemental livestock feed source following vegetable harvest. To the farmers, the disvalue of vegetable yield reduction was outweighed by the value of feed supply. This illustrates why it is important to assure that the physical damage from weed infestation is in fact translated into an economic problem. The effort required for effective biological control of nuisance weeds may not be justifiable from the point of view of the tactic's users.

It is the combination of all uses to which land is devoted (e.g. crop and livestock production, or drainage and recreation) that determines the land value and, thus, the disvalue of its infestation with weeds. All else equal, the greater the value of weed-infested land in its current uses, the higher the probability a biological control technique will be economically feasible.

The generally positive relationship between the value of losses from weeds and the economic feasibility of weed biocontrol is tempered by a negative relationship between the severity of damage per weed individual and the economic benefit of biological control. By its very nature, biological control allows a low, steady-state level of the weed population to survive. If the damage per individual in that steady-state population is high, even high rates of reduction achieved by the biocontrol agents may not be sufficient to drop the pest population below the economic injury level (Reichelderfer 1981). Weeds that cause moderate or low levels of damage per individual possess high economic injury population levels, require lower proportional control and, thus, are targets for which control is more likely to be economically feasible.

Availability and cost of current weed control. The economic feasibility of biological control is greatest in cases for which there is no other weed control option. The likelihood of economic feasibility also is high for the biological control of weeds for which current control costs are high. Agricultural weed control costs can include the effects of having to synchronize or delay field operations as well as the direct costs of herbicide materials and/or machinery, fuel and labor to apply materials or clean weed seed from products.

The opportunity cost of weed control (the value that time or managerial effort devoted to weed control could produce if engaged in other activities) can be very high, especially in less developed regions. The requirement of labor for weed control often limits the area of production in traditional farming systems (Koch *et al.* 1982). For example, in the maize/bean production systems of the Jinotega region of Nicaragua, averages of 13–37 man-days/ha are devoted to manual weeding. Labor for weeding represents 21 to 35% of total farm family labor available, there, for crop production (Tienhoven *et al.* 1982). (Koch *et al.* [1982] cite evidence indicating that from 30 to 61% of farmers' time in various African cropping systems is spent on weeding.) Labor is the factor that limits crop production possibilities in the Jinotega region (Tienhoven *et al.* 1982) and in similar regions where farm labor is mainly family-based. If labor required for weeding was reduced, additional hectarage could be cultivated and the income derived from farming much greater. Thus, although the market value of labor may be low, its value in relation to increased production possibilities can be quite high.

Both the direct and indirect costs of weed control in production enterprises need to be considered when assessing economic feasibility of biological control. If the sum of direct and indirect costs of current control is low, the potential feasibility of new alternative weed control methods also is relatively low.

Net effect of weed losses and control costs. Adding together costs of current control and value of losses that occur despite control efforts provides a measure of a weed's net impact on the target user group. Tradeoffs can occur between loss and cost factors in determining net effect. A weed population that causes moderate damage but is expensive to control may have as large an impact on the user as one that causes severe losses but is easy to control by current methods. The net economic effect of losses and costs under current control is the benchmark against which the expected net benefit of biological control needs to be compared.

Technical Effectiveness of Biological Control Option

A range of taxonomic and ecological characteristics of the target weed and potential biological control agent affect the probability that a given biological control technique will be a technical success in reducing the weed problem. Included among the factors DeLoach (1978) recommends should be considered in evaluating the biocontrol success potential for various weeds are whether the weed is: introduced or native; annual or perennial; a pest in a stable or disturbed habitat; and the site of origin of the weed genus, number of species of the weed genus in the control area, and the number and importance of related plant species in the area (DeLoach 1978). Harris (1973) and Goeden (1983) list and discuss a number of characteristics of insect agents that affect the potential success of an agent's use in providing adequate weed control. Many of the characteristics they identify, including phenology of attack, host specificity, extrinsic mortality factors, compatibility with other control agents, and evidence of effectiveness as a control agent, apply equally as well to consideration of higher animals or plant pathogens as biocontrol agents.

These characteristics of the weed and biocontrol agent are directly related to potential economic feasibility. As technical effectiveness increases and all else is constant, the probability that the technique is economically feasible improves. However, technical effectiveness should not be used as the sole basis on which to judge economic feasibility. Depending upon the costs required to achieve predicted effectiveness of control by biological means, and the relationship of the method's net returns to those obtained by current methods, a highly effective biological control technique may, or may not be economically feasible.

Pest Spectrum

An additional characteristic of the target weed — its relationship with coexisting weed problems — and host-specificity of the biocontrol agent interact to further affect economic feasibility of biological control of the weed. Simultaneous occurrence of several weeds of the same general type has a negative impact on economic feasibility of species-specific biological control techniques. If chemical or cultural methods can control all coexisting weed species of a certain type, and if the available biocontrol agent is specific to only one of these species, use of the biological control alternative, all else constant, will likely result in little or no relative benefit. Control action still would have to be taken against the coexisting weeds. If that action, like the use of a broad-spectrum herbicide, is both necessary and effective against all coexisting weeds, any cost of utilizing the biocontrol agent would be unjustified. Thus, economic feasibility of biological control is most likely to be found for singly occurring major weed species.

Variability and Rapidity of Biological Control Agent's Effect

Many potential weed control users will be as concerned with the variability of a biocontrol tactic's effect as they are with the average expected effect. A technique that consistently reduces weed populations by around 60% a year will be viewed as more desirable than one that reduces the weed population by 90% one-third of the time, 75% one-third of the time, and 20% one-third of the time, even though both give similar average control over time. Uncertainty about the technique's effect in a given time period increases the risk of employing it. Risk-averse users, especially, prefer consistency over the possibility of periodically outstanding effect. They will actually pay a premium (a higher cost) for a technique that has consistent results. The risk associated with using a highly variable biological control agent adds a user cost that adversely affects its economic feasibility.

Another characteristic of weed control that is valued by risk-averse decisionmakers is a quick and readily apparent reduction in the weed population. If for example, a biological control tactic requires the user to forego herbicide application over the period of time required for endemic establishment of a plant disease, the user may perceive that he or she is risking a loss by waiting for an uncertain benefit. This means the user cost of the technique is greater than its direct cash outlay requirements.

Risk and uncertainty are important features of economic feasibility. The more variable or otherwise risky a technique is viewed, the lower its economic feasibility from the perspective of its potential users.

User Costs of Biological Control

Obviously, the cost required to effectively employ a biological control technique weighs heavily in users' determination of the techique's economic feasibility. All else equal, the lower this cost to the user, the greater the economic feasibility of the technique.

In general, classical biological control is likely to require lower user costs than augmentative or inundative biocontrol techniques. However, even when the biocontrol agent is produced and distributed by a public body, free of direct charge to beneficiaries, some user costs may exist. This is particularly true for crop protection. Many of the component practices making up a cropping system influence or are influenced by weed infestation (Koch *et al.* 1982). When the status of a weed pest in a production system changes due to biological control, changes may have to be made in the date of planting, type or timing of tillage operations, methods of control for remaining pests, or other production practices to accommodate and preserve the benefit of the biocontrol agent. If, for example, the weed biocontrol agent is an insect that is susceptible to insecticides currently used against insect pests, the user may be faced with a tradeoff between weed and insect pest control. Since changes in production practices in turn can affect the yield and/or quality of the commodity being produced, such changes, and their effects, resulting from biological control need to be anticipated and assessed. While in some cases, they will result in a savings to the user, in others they will represent a cost.

Another factor to consider in determining whether or not beneficiaries of classical biological control will face new costs is the type of plant likely to fill the niche formerly occupied by the target weed. A proportion of the benefits of biocontrol may be superceded by new problems arising as other weeds increase to occupy the habitat (Harris 1980). Are the species most likely to replace the biologically controlled weed more or less damaging than the original weed pest? Are they more or less costly to control? The answers to these questions have important implications for the long-run cost and thus the eocnomic feasibility of a classical biological control possibility.

Augmentative biological control may, and inundative biological control most often does, involve direct cash outlay in addition to the possible opportunity costs of required changes in production practices. The market price of biological control materials for inundative use are determined by the value of the target weed's control (Bowers 1982). Thus, these materials are likely to be priced competitively with chemical herbicides. An advantage of host-specific materials is that the cost of applying them may be lower than for broad-spectrum materials. For instance, aerial applicators charge less to apply the spray formulation of fungal spore of *Colletotrichum gloeosporioidies* (Penz.) Sacc. f. sp. *aeschynomene* (Melanconiales) than to apply 2,4,5-T ([2,4,5-trichlorophenoxy] acetic acid) for control of curly indigo in rice fields near soybeans. This is because they don't have to assume the risk of killing the beans (Kidwell 1984).

While direct cost advantages may be available from inundative use of mycoherbicides, this tactic also can require costly changes in production practices. For example, to achieve adequate control of nutsedge by *Puccinia canaliculata* (Schw.) Lagh. (Uredinales), some farmers may have to alter their use of fungicides for crop protection (Phatak, cited in Kidwell 1984). By delaying fungicide application until the rust is well established, crop losses to other fungal diseases may increase. All user costs, both direct and indirect, need to be considered in the projection of a biological technique's economic feasibility.

Relative Net Returns — The Ultimate Measure

It is the comparison of benefits and costs of biological control with benefits and costs of current control that determines economic feasibility from the user's perspective. Economic feasibility is indicated when:

$$P[Q - f(DN)(1 - E_1)] - C_1 - g(V_1) < P[h(Q) - f(DN)(1 - E_2)] - C_2 - g(V_2)$$

where Q is the units of output (crop yield; animal carrying capacity; visitor days to parkland; volume of water flow; etc.) resulting from economic activity on uninfested land; P is the monetary value per unit of output; and f is the weed damage function, which reduces output as a function of D, the damage potential per individual weed, and N, the weed population density. E_1 is the percent reduction in the weed population achieved by current control, and E_2 is the percent reduction achieved by biological control. C_1 and C_2 represent the direct user costs of control by current and biocontrol methods, respectively. V_1 and V_2 are measures of the variability of current and biological control effects, respectively, and g is a function expressing how the user's attitude towards risk modifies the absolute value of benefits and costs. Finally, h is a function expressing how changes in current practices, required for effective biological control, modify output potential under uninfested conditions. This latter function represents the opportunity cost or benefit of changes in the output generating system.

Note that the comparison is made between current control and the biological alternative. The algebraic expression indicates that tradeoffs among cost, average effectiveness, and variability of effect of a weed control technique can be made without sacrificing degree of economic feasibility. For instance, a technique that has high user costs but low variability of effect may be as economically competitive with current control as one that has low costs and high variability.

Actual functional forms and absolute measures of the factors indicated in the algebraic equation most likely will not be available for use in quantifying economic consequences of a potential biological control technique at the point when research program decisions must be made. However, systematic, qualitative assessment of these factors and their interrelationships can be valuable in targeting for research particular weed–economic system–biocontrol agent combinations that are likely to yield economically feasible biological control techniques. Also, during experimental phases of a selected technique's development, the expected economic performance of the technique can be improved by attempting to optimize its application and increase the positive factors affecting economic feasibility (Taylor and Burt 1984).

If economic feasibility cannot be expected, even when a technique's management system has been optimized, it is doubtful that its target users will participate either in the technique's implementation or in the preservation of its potential benefits. If however, after factors affecting economic feasibility have been considered, a potential biological control technique is expected to be economically attractive to its users, it is useful to go beyond economic feasibility to examine the broader economic implications of the technique's implementation.

Beyond Economic Feasibility

While an economically feasible biological control technique may be judged a profitable alternative by users, a variety of commercial or societal factors may preclude its availability or overall desirability.

Potential for Commercialization

The feasibility and cost of providing effective commercial biological control products are especially critical to the success potential for inundative biological control of weeds. Market potential needs to be assessed on the basis of the area over which the target weed problem exists and could be controlled by use of the marketed product. If the product cannot be employed by a sufficiently large number of users to make production profitable, it will not be commercialized. If only a small number of potential users exist, the product may not be made available even if those users are anxious to apply it. Other economic considerations for commercialization of biological control agents include research and development costs, need for capital investment, product cost, royalty and patent requirements, and the return on investment expected from production and sales (Bowers 1982).

Public Intervention

Public intervention in biological control may be necessary or desirable under certain circumstances. If a technique is judged economically feasible by users, is expected to yield high benefits, but does not have good potential for commercialization, the public sector may assume responsibility for helping users capitalize on expected benefits. In many cases, particularly for classical biological control techinques, the effective use of natural enemies cannot be achieved by individual users. Some form of regional organization is necessary to expedite the biological control approach. Because neither beneficial nor destructive impacts of a widely distributed biological control agent can be restricted to those who are willing to pay for it, government involvement in classical or, in some cases, augmentative biological control is a necessity (Tisdell *et al.* 1984). It is for these cases that the entire range of social benefits and costs needs to be assessed following an indication that a biological control possibility is likely to be judged acceptable and economically feasible by its principal beneficiaries.

Societal Impacts

A variety of individuals and groups other than the primary user group may be impacted by biological control of weeds. These include individuals who directly benefit from unsolicited weed control for which they, otherwise, would not be willing to pay, as well as individuals who are negatively affected because they view or utilize the weed as a beneficial species. Consumers of the output affected by the controlled weed may benefit more than the producers of the affected output. In the case of public biological control programs, the cost to the taxpayers for supporting weed control must be considered. Credible accounting of the full societal impacts of the biological control of weeds must include estimates of gains and losses to all affected groups. Leaving out a set of gainers or losers will lead to erroneous calculation of net societal impacts. External costs and benefits and market impacts need to be fully assessed to determine who gains, who loses, and by how much.

Externalities. Costs and benefits accruing to individuals external to the biological control user group are termed externalities. Externalities can be negative (external costs) or positive (external benefits). Conflicts of interest in the value of weeds give rise to an important set of negative externalities (Andres 1981). A measure of willingness to pay to preserve the weed species, on the part of those who value its existence, is the relevant estimate of these external costs. Various methods are available to assess this willingness to pay (Yardas *et al.* 1982). Positive externalities may arise as biological control of the weed affects individuals who benefit from reduction in the population of a species not formerly recognized as a pest in their production system.

The net value of positive and negative externalities should be compared with direct net benefits enjoyed by the biological control user group. If the value of net benefits to gainers is larger than the value of negative externalities, society is said to be better off.

Market impacts. Estimating the full economic impacts of control of weeds in agricultural or other production systems further requires consideration of the potential response of the protected commodity's market. Reduced weed populations will increase yield and/or lower production costs for the affected commodity. If a large number of producers receive these benefits, increased levels of the commodity's supply may result. This stimulates a change in commodity prices. Production and consumption patterns respond, in turn, to the change in commodity price. The net effect of market interactions often will present large benefits to consumers of the affected commodity (Emerson and Plato 1978). These benefits can be of greater magnitude than the benefits accruing to producers. Bypassing estimation of the commodity price, supply, export, and other market changes arising from a major change in pest status will lead to misleading results with regard to the full economic impacts of the change (Kuchler *et al.* 1984).

Benefit–cost analysis. Benefit–cost analysis provides a useful framework for assessing total costs and benefits of biological control. Benefit–cost analysis should take into account money's future value and express the stream of private and public costs and benefits over time in a lump, present value measure (see chapter 5 of Reichelderfer *et al.* 1984). This assures benefits and costs are compared on a common basis.

Conclusions

Selection of a biological control tactic with high probability of economic feasibility involves a search for the following characteristics: 1. The individuals or group responsible for application and/or maintenance of the potential biocontrol approach perceive the target weed problem as a serious one; 2. The economic activity impacted by the weed has high value; 3. Taxonomic and ecological characteristics of the weed and the biological control agent are such that efficacious control by the biological method is indicated — but, the value of damage per weed invididual is not high; 4. The biological control agent's effect on the weed is neither slow nor highly variable; 5. There either is no current effective control available for the target weed, or current control is very costly; 6. Implementation of biological control does not require great expense by users, either in terms of cash outlay or the effect of a required change in production practices; and 7. The net economic returns to users of the biocontrol tactic are expected to equal or exceed those for alternative control.

The last of these characteristics is a function of the interaction of the six previous factors. Substitutability and complementarity among the first six factors listed can occur to make a biocontrol tactic possessing one or several undesirable characteristics a profitable alternative.

Economic feasibility of biological control of weeds can be expected under a range of conditions. It is most likely to be encountered for control of exotic weeds against which herbicides are ineffective or excessively costly. The probability of economic feasibility also may be high in developing regions where the resources of subsistence farmers are insufficient to support capital-intensive production practices and/or labor availability limits productive capacity (Greathead and Waage 1983).

Once indication of economic feasibility is obtained, the selection process can further be refined by considering the broader socioeconomic consequences of biological control tactics' development and implementation. Comprehensive accounting for externalities and market impacts of implementation is a difficult task that need not be undertaken if the biocontrol tactic is not first determined to possess probable economic feasibility. For, if the tactic's users do not have incentives to adopt, utilize, and/or preserve the benefits of biological control, the tactic's broader impacts are not likely to be realized.

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Bringing the Cost Benefit Analysis of Biological Control of *Chondrilla juncea* Up to Date

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Abstract

The cost benefit analysis of biological control of skeleton weed conducted in 1976 is re-examined in the light of recent field data. The decline of the common form of the weed has not differed significantly from that predicted, except in the driest regions, but the density and distribution of the two other forms have increased more than was assumed. This, together with the lack of effective biological control to date, has diminished the predicted returns slightly. The methodology is described, which takes account of different weed densities and varieties, and the effect of regional differences in rainfall and crop rotation on control methods and on yield reductions produced by the weed. The applicability to other weeds and predictions of benefit is briefly discussed.

Mise a Jour de l'Analyse Coûts-Avantages de la Lutte Biologique Contre *Chondrilla juncea*

L'auteur examine deux importantes hypothèses issues de l'analyse coûts-avantages de la lutte biologique menée en 1976 contre l'herbe squelette, à la lumière des données recentes rassemblées sur le terrain. La réduction réelle de la forme commune de la plante nuisible ne diffère pas de façon notable des prévisions, sauf peut-être dans les régions les plus sèches, mais la densité et la distribution des deux autres formes ont augmenté plus qu'escompté, ce qui, compte tenu de l'inefficacité de la lutte biologique jusqu'à ce jour, n'a pas permis d'obtenir les avantages prévus, bien que l'écart ne soit pas marqué. Le document expose la méthodologie qui, en plus de tenir compte des différentes densités et variétés de plantes nuisible, examine les différences régionales relatives à la quantité des précipitations et aux méthodes d'assolement et leurs effets sur d'autres méthodes de lutte et sur la baisse de production provoquée par la plante nuisible. Le rapport examine bienement les possibilités d'application à d'autres plantes nuisibles et les avantages prévus.

Introduction

During 1975–76, as part of an inquiry by the Australian government into the financing of rural research (Anon. 1976), a cost benefit analysis was carried out of several programs of the CSIRO Division of Entomology, including the program for the biological control of skeleton weed, *Chondrilla juncea* L. (Compositae). The data on which this analysis was based and its main conclusions and predictions were given by Cullen (1978) and Marsden *et al.* (1980).

While an entirely new analysis with the benefit of hindsight is slightly premature, it seems valuable at this stage to update the biological basis of the analysis and to examine the predictions made earlier in the light of the field data now available. This review should also indicate what more data are required for a later, comprehensive re-analysis as well as perhaps some pointers of a more general nature.

Methods

C. juncea has several economic effects (Marsden *et al.* 1980), the most important by far being that on the wheat industry. The root system of the weed competes very effectively with wheat for both nutrients and moisture, the most serious effect coming in the very early stages of wheat growth. Later in the season, the tall, wiry stems interfere with harvesting machinery. This problem may be reduced by early spraying, but the competitive effect is more intractable and constitutes the major part of the problem. In the 1972–73 season, the last before any influence of biological control, total losses to the wheat industry in southeastern Australia were estimated at $20.037 million, of which $18.579 million was due to lost productivity and $1.458 million to spraying costs (Marsden *et al.* 1980).

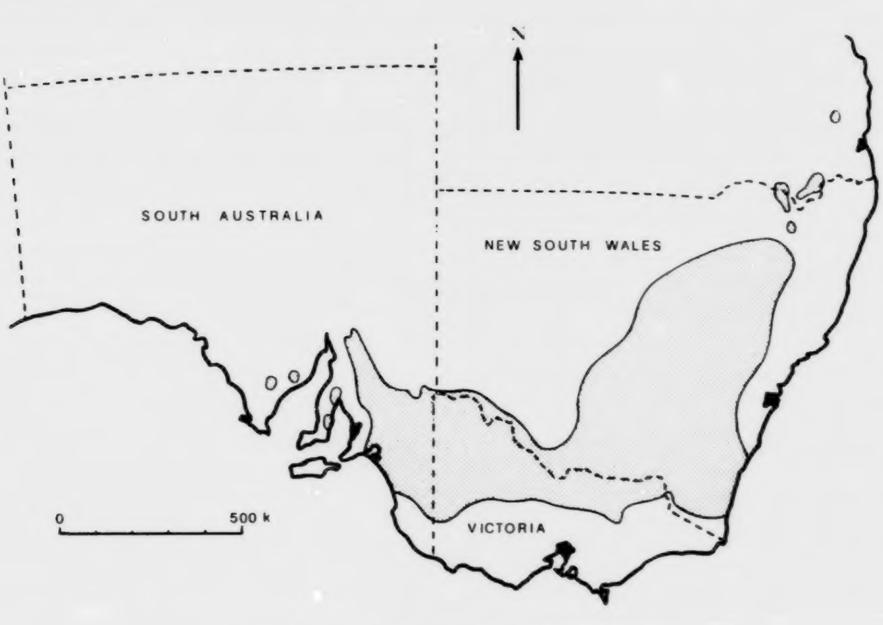

Fig. 1. Distribution of *C. juncea* L. in S.E. Australia.

Marsden *et al.* (1980) have described the method used for calculating these estimates. The weed's distribution was divided into regions with similar characteristics with regard to density, management practice and form of *C. juncea* involved. For each of the three States principally concerned (Fig. 1), a series of regions was defined so as to include a group of statistical subdivisions, for which annual figures for wheat production and area planted were available. The distribution of the weed was divided into regions of differing infestation levels (heavy, medium, light, Fig. 2) and similarly into regions of differing probabilities of control by pasture management, the best alternative system (Fig. 3).

The critical relationship between infestation level and the estimate of economic loss must accommodate the changes in density which have been monitored since the introduction of biological control agents. Table 1 illustrates the relationship used, the result being an overall loss factor typical for each region, which varies according to moisture availability each year.

The use of pasture management for control implies that part of the wheat crop is not subject to losses due to *C. juncea* and is also not sprayed. For the present analysis, it has been assumed that these areas and their effects on calculating losses from the weed have remained as detailed in Marsden *et al.* (1980).

The State of New South Wales (N.S.W.) was again subdivided according to the degree to which each form of the weed contributed to the problem. The principal biological control agent, the rust *Puccinia chondrillina* Bubak & Sydow (Uredinales), only attacks the most widespread form of the weed (Cullen 1974), form A (Hull and Groves 1973), whereas significant populations of all three forms occurred in N.S.W. Regions were therefore designated according to whether form A made up 100%, 50%, or 20% of the problem (Fig. 4) and loss factors following biological control, corrected accordingly.

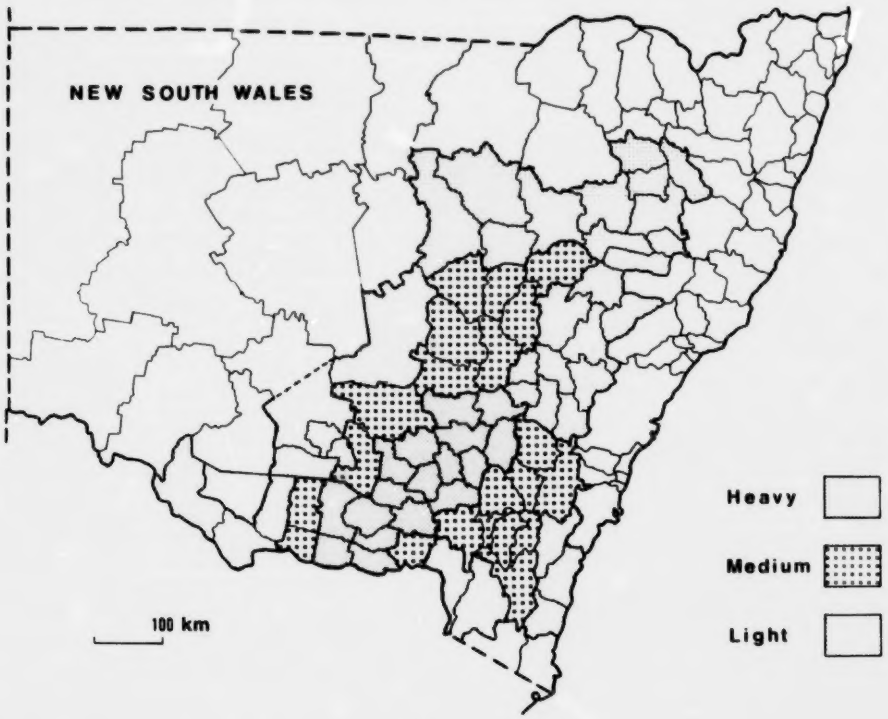

Fig. 2. Statistical subdivisions of New South Wales showing division into regions according to level of infestation of *C. juncea* L.

Production losses were calculated for 1972–73 using the overall factors modified for each region and then for 1973–74 using new loss factors modified to take into account the two principal effects of the control program. Experimental work (Groves and Williams 1975; Cullen unpubl. data) suggested that biological control reduced the competitive effect of the roots of *C. juncea*, and therefore the losses, by at least 25%, the reduction being maintained throughout subsequent seasons. Secondly, the decreases in density in the field were incorporated into the distribution of densities characteristic of each region (Table 2) and new loss factors calculated. Using these and actual production figures for 1973–74, potential production in the absence of the weed was calculated. Actual production loss due to the weed in the presence of biological control, and the potential loss due to the weed in the absence of biological control could thus be derived, and savings and percent of the problem solved could be calculated. Using field data and estimated production figures, calculations of percent of the problem solved were made for 1974–75 and 1975–76. The trend obtained for increasing percent of the problem solved with time was then projected to a final control level of 90% in 1979–80. Form A of the weed was calculated to represent 88% of the problem at the time, and thus a final estimate of 79% of the total problem solved could be deduced (Marsden *et al.* 1980).

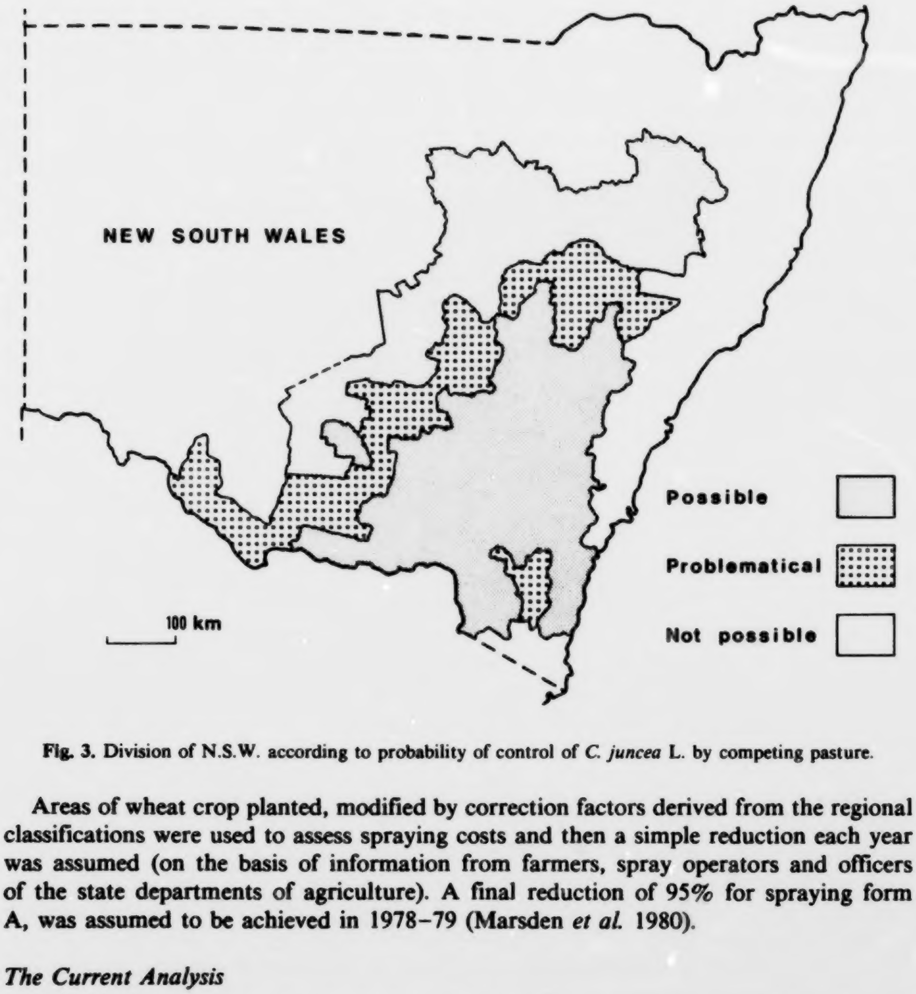

Fig. 3. Division of N.S.W. according to probability of control of *C. juncea* L. by competing pasture.

Areas of wheat crop planted, modified by correction factors derived from the regional classifications were used to assess spraying costs and then a simple reduction each year was assumed (on the basis of information from farmers, spray operators and officers of the state departments of agriculture). A final reduction of 95% for spraying form A, was assumed to be achieved in 1978–79 (Marsden *et al.* 1980).

The Current Analysis

The changes in percent wheat crop infested at different densities during the seasons subsequent to 1975–76 were estimated from experimental plot data and field records (Table 2). The most recent complete set of agricultural statistics was for the season 1978–79, a season of adequate rainfall and high production levels. The overall loss figures were calculated from Table 2 and calculations made of actual loss, potential loss, savings and percent problem solved. Estimates of the percent problem solved in 1979–80 and 1980–81, the period covering the predicted levelling-off point, were calculated using the 1978–79 production figures, but with the field data from the later seasons.

Results and Discussion

The percent problem solved for the seasons 1978–79, 1979–80 and 1980–81 is presented in Table 3, along with the values predicted by Marsden *et al.* (1980).

Table 1. Relationship between level of *C. juncea* L. infestation and yield loss[1].

Infestation	% wheat area	Weed density plants m^{-2}	Yield loss %			
			Wet year		Dry year	
Heavy	20	> 100	50	$\bar{x} = 18$	80	$\bar{x} = 32$
	20	10–99	30		50	
	20	1–9	10		30	
	40	< 1	0		0	
Medium	20	10–99	30	$\bar{x} = 8$	50	$\bar{x} = 16$
	20	1–9	10		30	
	60	< 1	0		0	
Light	20	1–9	10	$\bar{x} = 2$	30	$\bar{x} = 6$
	80	< 1	0		0	

[1] Modified from Marsden *et al.* (1980).

The success in solving the problem due to form A of the weed was slightly less than predicted. A breakdown into the State of N.S.W. on the one hand and the States of Victoria and South Australia (S.A.) on the other, shows that control was better than predicted in N.S.W., but clearly worse in Victoria and S.A. The *C. juncea* infested areas of the wheat belt in Victoria and S.A. are distinctly drier and with lighter, sandy soils than those in N.S.W. By 1976, population decline was already slower in Victoria and S.A. and it seems this might eventually be correlated with lower levels of control. While the population decline observed in 1976 continued as predicted or more steeply in N.S.W., it continued only until 1978–79 in the drier areas and a slight increase was noted in 1979–80 and 1980–81. *P. chondrillina* was less common in these two seasons, particularly in 1980–81, the first of a series of drought years. This drought only broke in 1983 so it may yet take some time to achieve the final level of control. If a level close to that of 1978–79 (i.e. approximately 80%) is achieved, overall control of form A will be fairly close to that predicted. It will have required longer, which suggests that the predicted approach to the final asymptote should have been more gradual.

For comparisons with the earlier prediction, the percent problem solved has been used, hence avoiding problems of differing dollar values and market prices. In actual 1979 values, the saving in reduced production losses for the 1978–79 season was $48.928 million.

The prediction that spraying for *C. juncea* would have reached 5% of the original by 1978–79 was also slightly optimistic. A survey in S.A. in 1977 (A.F. Tideman, pers. comm., 1977) suggested that in the drier areas reduction had been substantial, but less than predicted. With higher reductions in N.S.W., it is likely that the overall 1978–79 rate was closer to 10% of the original.

The Influence of the Other Forms of *C. juncea*

In order to obtain projections to the year 2000, Marsden *et al.* (1980) made the following assumptions: (a) strains of *P. chondrillina* effective against the other two forms of the weed would be found in Europe and imported during 1978–79; (b) the subsequent development and level of control achieved by these strains would be similar to that of the first strain; and (c) in the meantime, increase in the other forms would be insignificant.

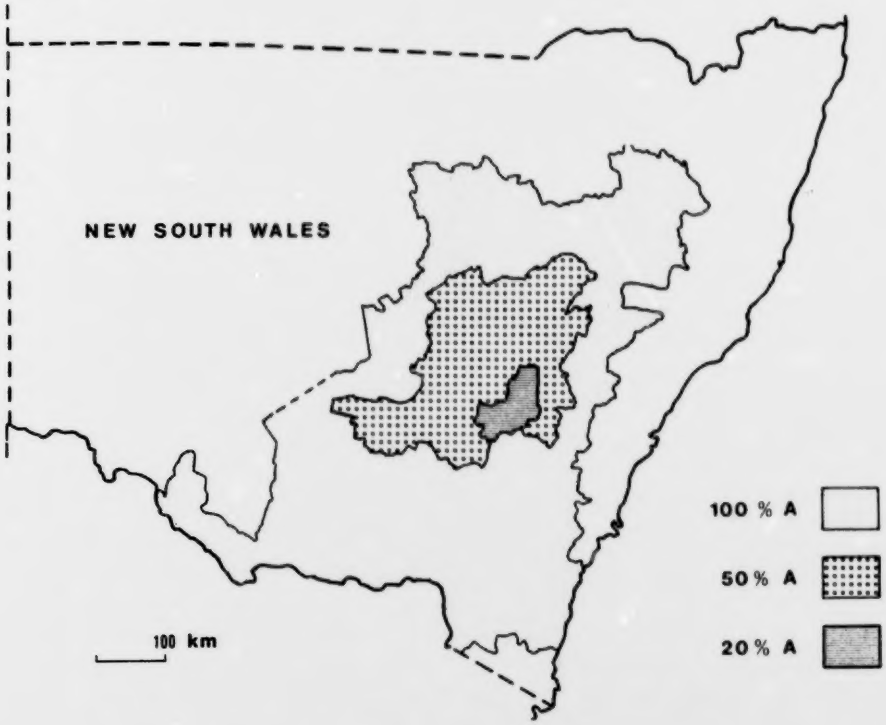

Fig. 4. Division of N.S.W. into three regions according to the importance of form A in the problem created by *C. juncea* L. (100%, 50%, or 20%).

In fact, not until 1983 was there a successful field colonisation of a strain potentially effective against one of the other forms (form B), and a virulent strain for form C is still lacking. Thus there are no small increases in benefits, as predicted from the 1980–81 season on, which could be added to the 79% problem solved already attained (Table 3). More importantly, with increasing time, the increases in form B and C are no longer insignificant.

Changes to 1980, recorded by Burdon *et al.* (1981) include an increased distribution of these forms within the area occupied by the weed in southeastern Australia, very large changes in the proportions of each of the three forms along a transect in N.S.W. and a detailed roadside survey suggesting a 100% increase in forms B and C between

1977 and 1980. While the figures for 1978–79 (Table 3) should not be significantly affected, the later seasons should take this increase into account. Accurate distribution data, needed to define new categories and regions, are not yet available. Nevertheless, the data of Burdon *et al.* (1981) suggest that an approximation for 1980–81 could be obtained if it is assumed that: (a) in areas where forms B and C represented 50% or 80% of the weed (Fig. 4), the proportion is now 90%; (b) with the increase in density, all such infestations are now in the medium category (no infestation of these forms has been observed which would be classified as heavy); and (c) savings are reduced by 10% over the whole area previously classified as having only form A, due to invasion by the other forms.

On this basis, the figures for 1980–81 give an overall problem reduction of 61.2%, compared with 70.5% in Table 3. Since 1980, the main change has been a gradual increase of forms B and C within the region previously classified as 100% form A.

Table 2. Changes in % wheat crop infested by different densities of *C. juncea* L.[1]

States	Weed density (no./m^2)	1972	1973	1974	1975	1976	1977	1978	1979	1980
N.S.W.										
Heavy	100	20	6	6	0	0	0	0	0	0
	10–99	20	34	17	25	11	0	0	0	0
	1–9	20	20	37	24	36	42	35	12	12
Medium	10–99	20	20	10	5	5	0	0	0	0
	1–9	20	20	30	24	22	22	15	5	5
Light	1–9	20	20	20	14	7	7	0	0	0
Vic. and S.A.										
Heavy	100	20	14	6	0	0	0	0	0	0
	10–99	20	26	34	30	16	12	0	12	18
	1–9	20	20	20	30	39	31	38	21	27
Medium	10–99	20	20	20	10	10	5	0	5	5
	1–9	20	20	20	30	25	25	25	15	20
Light	1–9	20	20	20	20	15	15	15	10	10

[1] Figures for 1972 are based on counts in winter–spring 1972 and apply to the 1972–73 season, those for 1973 are for 1973–74, etc.

As a result, spraying has also increased again slightly in Victoria and S.A. above the 10% level suggested for 1978–79.

Conclusions

This brief re-examination of skeleton weed control suggests the following points.

The prediction regarding the decline of form A was reasonably accurate though the final equilibrium will take longer to reach than predicted.

The influence of forms B and C of the weed has been more significant with increasing time than predicted, suggesting that more account should have been taken of less optimistic possibilities. However, even the worst scenario (i.e. a complete take-over by these forms) would take a long time to eventuate, by which time the accumulated benefits would be enormous.

In reality, providing a strain virulent against form C of the weed can be found fairly soon, the ultimate effect on the overall analysis is likely to be minimal. This, plus the economic scale of the damage still being caused, emphasises the importance of pursuing the search for virulent strains of *P. chondrillina*.

On a more general note, questions regarding long term benefits will be increasingly asked of biological control programs, and realistic models are needed to estimate the effect of varying parameters, e.g. rate of population decline. To allow analysis and representation of the problem, information on the following points seems to be the most important: (a) the relationship between economic loss and the abundance of the weed (density, cover, ranking system, etc.), which can be reliably monitored and related to possible control effects; (b) the variation in this relationship according to types of economic effect, geographical region and season; (c) next best control procedures; and (d) other relevant scenarios, e.g. replacement by other weeds.

The present exercise is an example of an approach which has been, and can be used, to make forecasts regarding the outcome of a program, given an observed or assumed level of effect by biological control agents. However, the prediction of a level of effect will clearly depend on relevant research and biological control theory. As the demand for economic prediction and assessment increases, then the need for relevant research becomes even more crucial.

Table 3. Reduction (%) of the problem of decreased production due to *C. juncea* L.

Years	Considering form A only				Total problem (forms A+B+C)			
	N.S.W.	Vic. & S.A.	Total	Predicted	N.S.W.	Vic. & S.A.	Total	Predicted
1978–79	88.2	80.3	84.1	87.0	68.2	80.3	73.7	76.5
1979–80	95.8	74.2	86.2	90.0	74.0	74.2	75.5	79.0
1980–81	95.8	66.3	80.4	90.0	74.0	66.3	70.5	81.5

Acknowledgments

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Field Applications of Biological Control — Implementing the Research

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Abstract

An effective biological control program at the state or province level requires a well organized effort once research studies have been completed and an organism is approved for field release. Too often implementation is lacking and biocontrol projects never reach their full potential of effectiveness. Best results are obtained where a lead agency has the responsibility for overall program delivery including program awareness, and increase and distribution of organisms. The public wants biological control! This is particularly true of government agencies responsible for the management of large tracts of land and which are facing increasing restrictions on the use of herbicides. We need coordinated efforts designed to make the most of the research being provided.

L'Application sur le Terrain de la Lutte Biologique — Implémentation de la Recherche

Pour être efficace, au niveau de l'état ou de la province, une lutte biologique exige un effort bien organisé, dès que la recherche est achevée et que l'élargissement d'un organisme a été recommendée. Trop fréquemment, la mise en oeuvre manque et les luttes biologiques n'atteignent jamais leur grand potentiel d'efficacité. On obtient les meilleurs resultats où une agence directrice est globalement responsable du programme entier, y compris la publicité et l'élevage et la répartition d'organismes. C'est le public qui veux la lutte biologique. Ceci est vrai en particulier dans le cas des agences de gouvernment qui sont résponsables de la gestion des terres étendues et se trouvent face de plus en plus des restrictions sur l'emploi d'herbicides. Nous avons besoin d'efforts co-ordinés de nature à tirer le plus grand profit de la recherche disponible.

Biological control of weeds is a field of endeavour which has developed rapidly in recent years. The number of individuals involved in research is increasing every year and the general public has become quite aware of this control technique. Unfortunately in many cases, biological control programs are not being fully implemented at the state level (I will limit my comments to the U.S.A., since I am not familiar with the situation in other countries). Too often, one individual who has research and teaching responsibilities with a state university is expected to rear, collect, distribute and assess biocontrol organisms statewide. Granted the person will usually receive some assistance from country personnel, but one can only be expected to effectively handle a few weed projects when operating in this fashion. U.S. Department of Agriculture personnel are too few, and too involved in research, to be expected to be a factor in implementing programs at a local level. Country weed control personnel and extension agents can, and do, get involved in distribution of organisms, but this is generally a secondary function and they may lack expertise or equipment and facilities required for some programs. For these and other reasons, we often see research programs which have been developed for biological control either not being utilized, or at least not utilized to their fullest extent.

Having been involved in both research (with the USDA) and field implementation of programs (with the Oregon Department of Agriculture), it seems to me that a lead agency with responsibility for applying research developments is necessary if the maximum benefits are to be realized in biological control programs. Several states have certain elements of a program, but few are able to offer a complete service. The California Department of Agriculture has a fairly strong program which also includes work on the biological control of insects; Montana has recently developed a rearing facility for increasing certain species of insects; and the Oregon Department of Agriculture has a relatively strong weed program for the collection and redistribution of insects, but does little in the way of rearing. These are but a few examples of state programs, there are many others of one sort or another, but I am not aware of any which have a really complete service.

The general public has become quite aware of biological control in recent years and they like the idea. I seldom go to a meeting of farmers and ranchers without someone asking 'Haven't you got a bug for this weed?'. Television, radio and newspapers use biological control items as human interest stories (or fillers) so that the urban population is often as informed as the agricultural community. Some of these people are opposed to the large scale use of pesticides (except on their lawns and gardens). As voters, they support environmentally oriented legislators, who in turn can help to support biological control programs in funding appropriations. Public agencies, such as the U.S. Forest Service and Bureau of Land Management, which are responsible for the management of millions of acres of public lands, are very much interested in biological controls. The State of Oregon contains over 62 million acres, and more than half of that is public land administered by public agencies. In March 1984, a ban was imposed on the use of herbicides on those federal lands. Several other western States were similarly affected by the ban and subsequent actions. Thousands of acres of these public lands are infested with weeds such as diffuse knapweed, *Centaurea diffusa* Lam. (Compositae), and tansy ragwort, *Senecio jacobaea* L. (Compositae), seriously reducing their value for grazing. In addition, public agencies have been increasingly criticized for serving as a source of weeds which can spread onto private farms and ranches. Certainly it is not economically or environmentally feasible to conduct large-scale herbicide applications to help alleviate weed problems on thousands of acres of public lands, and for these reasons public agencies are seeking help through the use of biological control whenever possible. With the interest and demand for biological controls just described, there is a definite need for well organized state programs to implement the results of research studies. Generally, I believe this function should be the responsibility of State Departments of Agriculture. We cannot wait for token releases of organisms to increase and spread naturally at their own speed.

Of course the rate of spread and amount of effort required for distribution varies from organism to organism, and certainly insects such as *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on diffuse knapweed have spread rapidly throughout portions of Canada and the northwestern United States with a relatively small amount of human effort being required. On the other hand, it appears that the root-feeding beetle, *Sphenoptera jugoslavica* Obenb. (Coleoptera: Buprestidae), also for diffuse knapweed, will require considerable effort to achieve widespread distribution. The weevil *Phrydiuchus tau* Warner (Coleoptera: Curculionidae) for Mediterranean sage, *Salvia aethiopis* L. (Labiatae) is very slow to spread if left to its own devices. When asked about this insect, I usually describe it as 'looking like a bird dropping, but it moves slower'. We have been redistributing *P. tau* for several years and, while it is only partially effective in controlling Mediterranean sage, it should be considered as an integral part of a biological control program against the plant and should be spread throughout the range of Mediterranean sage. The cinnabar moth, *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae) on tansy ragwort was first introduced into Oregon in 1960 and had colonized and increased to the point of being harvestable by 1965. During the next 10 years, extension service personnel did distribute and establish a fair-sized number of new colonies, but not nearly the numbers required. This is not a criticism of the extension service; their personnel performed this service as a secondary function in their already overburdened work schedule, and they simply did not have the time required to do more. The Oregon Department of Agriculture biological control unit was formed in 1975, and since that time our personnel have distributed millions of cinnabar larvae, so they are now established over about three million acres of tansy ragwort infested land in western Oregon. Natural spread of the cinnabar moth is quite slow and widespread distribution requires considerable time and effort. In addition to our crews (primarily student summer employees), the general public is very aware of the program and many cinnabar larvae have been moved by private individuals.

Originally we believed that the tansy ragwort flea beetle, *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae) would spread much more quickly than the cinnabar moth. This has not happened. The beetles are established in many areas of western Oregon, and they are exerting considerable control on the plants in local situations, but in most cases they have not moved any great distances. Once tansy ragwort has been controlled at a site, the beetle populations tend to crash rather than spread significantly. This may be due to the dense forest vegetation which covers much of western Oregon acting as a barrier to mass dispersal by the beetles. While the cinnabar moth is very widespread it offers only partial control of the plant and populations are sporadic from year to year. A combination of the cinnabar moth and flea beetle has given us excellent control and we are distributing the flea beetle as quickly as our populations allow. While the cinnabar larvae are large, colorful, and easily collected and the public has been involved in distribution, the flea beetle is more difficult to collect, requiring the use of D-Vacs and aspirators, and distribution has largely been done by Department personnel.

Even organisms which do possess the capability to spread well naturally may require some continuing management. *Chrysolina quadrigemina* (Suffr.) (Coleoptera: Chrysomelidae) was introduced into the western United States during the mid-1940s to control St. John's wort, *Hypericum perforatum* L. (Clusiaceae), and the program became a classic in the annals of biological control of weeds. The beetles spread quickly, were effective against the weed, and achieved a high degree of control of St. John's wort over much of the western United States. However, in recent years, beetle populations have been low in parts of Oregon (and other states) and the plant has been able to rebound to a certain degree. The reasons for *C. quadrigemina*'s decline are unknown to me; perhaps long-term weather conditions have been unfavorable, or in some areas, large-scale grasshopper spray programs may have been detrimental. Whatever the cause, we do collect and distribute beetles to some new sites each spring and have been doing so for about the last five years. Thus, there is still the need for the continuing management of a long-established organism.

Biological control is not magic. Unfortunately, many in the agricultural community often have the idea that once a biocontrol organism has been released, their weed problems are over. Most successful projects will require a considerable amount of time and effort if they are to be utilized to the maximum extent. *C. quadrigemina* was a pioneer program in the United States, and was an almost immediate success. It sort of 'got the ball rolling' for future programs. I believe that many would agree that while there was considerable time and expertise put into that project, there was also a little bit of luck involved. I have to wonder: if the first program had been for Mediterranean sage using *P. tau* ('moves slower than bird droppings'), would biocontrol of weeds have continued? I suspect that the amount of effort required to implement such a program may have spelled doom to biocontrol of weeds in the U.S.

Implementation of programs does require some abilities beyond simply distributing organisms. In some cases, insectary rearing would be beneficial. One of the early bottlenecks in many projects is the limited supply of organisms available for initial field colonization, and with the increased demand for initial colonies, the problem is getting worse. Many insects do not lend themselves to laboratory rearing, but some can be reared and this could help to alleviate the problem. In Oregon we have minimal rearing facilities, and have done little rearing work, but we have recently received laboratory-reared larvae of *Calophasia lunula* (Hufn.) (Lepidoptera: Noctuidae) for release on Dalmation toadflax, *Linaria dalmatica* Mill. (Scrophulariaceae) from the USDA laboratory in California, and from the State-sponsored laboratory in Corvalis, Oregon. One thing we are considering is the development of 'weed farms' for initial field releases and increase of organisms. In this fashion we could intensely manage the plantings and have a continual supply of good quality plants at the right stage of development, rather than relying on field sites which are unprotected and may suffer from competition with other plants, grazing animals, fire, or any number of other undesirable factors. *L. jacobaeae* on tansy ragwort and *Urophora cardui* (L.) for *Cirsium arvense* (L.) Scop. (Compositae) are two species with which we will probably try this technique.

The Oregon Department of Agriculture is not a research organization. We do some rather superficial studies (which have been termed 'quick and dirty') on the effectiveness of certain organisms, but we rely on others for in-depth research. We cooperate with Oregon State University entomology and weed-control personnel on a number of programs and to a lesser extent with research scientists from the USDA laboratory in Albany, California. We have the responsibility for initially introducing and colonizing available organisms and later managing and implementing the programs as they progress. Our group was originally formed to distribute cinnabar larvae, but we have since become involved with 18 species of insects on 13 different weeds (the projects are in various stages of development). We have the State fairly well organized and receive good cooperation at the county and private land owner level. We have worked to create public awareness of biological control, and during periods of high cinnabar larvae populations, it is not unusual for us to receive calls from irate housewives wanting us to send out collection crews to get cinnabar larvae which are either crawling up the sides of houses or drowning in swimming pools. The encouraging thing about such a situation is that the housewives are aware of the program and they want the insects saved and utilized rather than spraying them.

In visiting with colleagues from various states regarding the development of an implementation program, their most frequent concern is lack of funding to hire the necessary personnel. Oregon's program was originally funded as a demonstration project by federal funds which were made available to states to use at their discretion. Within a few years, the State legislature appropriated money to continue the program and it has grown from there. In the late 1970s, the Bureau of Land Management and the U.S. Forest Service contracted with us to supply biological control services, mainly on tansy ragwort. We still maintain those contracts and have added several other lesser contracts in recent years. At the present time, our program is about 50% funded by the State of Oregon and 50% by outside sources. We are not strictly a biological control unit, but rather have responsibility for all Department of Agriculture weed control activities. We do some weed survey work as well as conducting limited herbicide applications. We offer a fairly complete 'weed service program' and for this reason we have been able to attract more contracts; however, the bulk of our contract funds are for biological control. Although I don't know this for certain, I suspect it may be easier to obtain funding for implementing programs than it is for research. As mentioned earlier, the large federal agencies charged with administering public lands are very much interested in biological control. They continue to receive increasing pressure against the use of herbicides (as evidenced by the current ban) and are seeking viable alternative measures for weed control. They sometimes do not possess the time or expertise necessary to conduct programs, and in many cases it is cheaper for them to contract with an established organization than to maintain their own staff. If funding is obtained from outside sources, we need to be able to produce results to maintain credibility. Fortunately for us in Oregon, we have had the tansy ragwort insects available and they have supplied us with a certain degree of success and helped maintain the confidence of our contractors.

I do not mean to imply that Oregon's program is perfect; certainly it is not, but we are expanding and hopefully improving each year. We would be happy to share our experience with anyone interested, and are willing to help supply insect colonies whenever we have them available.

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Narrow-leaved Hawk's-beard (*Crepis tectorum*) — Its Suitability as a Target Weed for Biological Control

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Abstract

The density of and losses in yield in terms of quantity and quality due to narrow-leaved hawk's-beard (*Crepis tectorum*) (NLHB) were investigated in fields of perennial forage crops located in the Parkbelt Region of Saskatchewan and the Peace River Region of British Columbia. NLHB was most frequent in mixed perennial forage crops. In alfalfa (*Medicago sativa*) fields, NLHB constituted only 5% of the biomass in 1982 and 1.2% in 1983. In first year alfalfa plots including replicates with and without NLHB, there were no significant differences in yield. Although excellent control was achieved in creeping red fescue (*Festuca rubra*) by the use of herbicides no significant increases in the yield of seed could be shown. Therefore, NLHB seems to be an excellent colonizer but a weak competitor. In 1983, less than 2% of the pollen collected from the middle of June to 13 July originated from NLHB. These results, based on data collected in only two years, suggest that NLHB does not warrant the relatively large expenditure of a biological control of weeds project.

La Mauvaise Herbe *Crepis tectorum* (Narrow-leaved Hawk's-beard) — Sa Convenance Comme Cible de la Lutte Biologique

On a recherché la densité du *Crepis tectorum* (narrow-leaved hawk's-beard, NLHB) et les pertes, en termes de rendement et de qualité, dûs à cette mauvaise herbe dans des champs de fourrages vivaces, situés dans la région 'Parkbelt' de Saskatchewan et de la région 'Peace River' de la Colombie britannique. La fréquence du NLHB était le plus élevée dans des fourrages mixtes. Dans des champs d'alfalfa (*Medicago sativa*), le NLHB n'a formé que 5% de la biomasse en 1982, et 1.2% en 1983. Dans des plantations d'alfalfa de première année, y compris des replicats avec ou sans NLHB, il n'y avait pas de variations significatives de rendement. Quoique la lutte contre le NLHB dans des plantations de *Festuca rubra* (creeping red fescue), au moyen d'herbicides, ait donné d'excellents résultats, on n'a pas pu montrer des augmentations significatives de rendement des graines. Ainsi, le NLHB parait être colon excellent mais compétiteur faible. En 1983, moins de 2% du pollen recolté entre le mi-juin et le 13ième juillet provenait du NLHB. Ces résultats, basées sur des données recoltées en deux années seulement, indiquent que le NHLB ne justifie pas la dépense assez grande d'une lutte biologique.

Introduction

A biological control of weeds project requires 10–20 years to complete and costs at least $2 million (Harris 1979). To warrant such expenditure it is important to first establish that a weed is causing sufficient crop losses.

Narrow-leaved hawk's-beard (NLHB) (*Crepis tectorum* L.) (Compositae) often becomes very prevalent and showy in the first year after sowing and in poor stands of perennial forage crops (Van den Born 1972). The purpose of this paper is to determine crop losses from this weed, in particular in alfalfa (*Medicago sativa* L.) (Leguminosae) and mixed perennial forage crops and to determine the general suitability of this weed for biological control with insects.

Origin and Distribution in Canada

NLHB is a herbacious annual or winter annual of the family Compositae with a deeply penetrating root system. It was introduced from Eurasia prior to 1890 (Babcock 1947; Darwent and McKenzie 1978). According to Najda *et al.* (1982) it occurs in every Province of Canada except Newfoundland. In Manitoba it may be found in isolated locations in all regions and it is particularly frequent from the U.S. border north to Dauphin (Thomas 1978*a*, *b*, 1979; Thomas and Wise 1981). In Saskatchewan, it is frequent in the Parkbelt region north of latitude 51° (Thomas 1976, 1977, 1978*a*, *b*, 1979). In Alberta, moderate to heavy infestations occur north of Olds (latitude 51°47′) (Dew 1981) including the Peace River region of British Columbia (Thomas and Wise 1983).

Biology

NLHB grows as a winter or summer annual depending on the date when seedlings emerge (Darwent and McKenzie 1978). In general winter annuals bloom earlier than the summer annuals. The blooming period extends from May to October with a peak in July. NLHB requires a long daylength to flower.

Materials and Methods

Occurrence in Alfalfa-brome Hayland

In 1982 and 1983, surveys were conducted in all agricultural districts of Saskatchewan where NLHB was reported to occur frequently (Thomas 1976, 1977, 1978*a*, *b*, 1979). At least one hayfield containing smooth brome (*Bromus inermis* Leyss.; Gramineae) and at least 5% alfalfa was surveyed in each agricultural district. Fields were selected by surveying the first field encountered when driving into a new agricultural district. Twenty 0.25 m^2 samples were taken using the method described by Thomas (1976). In 1982, only the number of seedlings of NLHB were recorded, and in 1983 the number of seedlings, the area covered by NLHB, other weeds (including grasses) and alfalfa in each 0.25 m^2. A total of 12 fields was surveyed in 1982 and 18 in 1983.

Biomass Sampling in Alfalfa

For this study alfalfa fields, used in the dehydration industry, were surveyed just prior to the first harvest of the season. The goal was to survey at least four fields under contract by each of the dehydration plants in Choiceland, Arborfield and Tisdale, Saskatchewan. A total of 13 fields was sampled in July 1982, 14 in June 1983, and 12 in July 1983. Fields were selected by asking the operators of the dehydration plants for the location of fields ready to be harvested in the next few days. In each field 20 samples, 0.25 m^2 in size, were taken. The quadrats were selected according to the method described by Thomas (1976), with the exception of one field with a uniform infestation of NLHB. Only 10 samples were taken in this field. The vegetation was clipped, separated into alfalfa, NLHB, and other weeds, dried at 100°C for 24 h, and weighed. At the time of surveying, samples of NLHB were collected in the Choiceland, Arborfield and Tisdale areas, packed in ice for transport to the laboratory, where they were frozen at −15°C. The samples were freeze dried, pulverized with a Thomas Mill, passed through a 0.5 mm sieve, and then analysed for their content of carotene, crude protein and crude fibre. (Association of Official Analytical Chemists 1970.)*

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*Analysis carried out by the Alfalfa Dehydrators Research Laboratory, Tisdale, Saskatchewan. Director Dr. Dale Pulkinen.

Hand-weeded Plots of Alfalfa and NLHB

Plots were established 20 km south-west of Melfort, Saskatchewan to follow population changes in NLHB and to determine its effect on the yield of alfalfa. Alfalfa (variety Beaver) was seeded in the fall of 1982 in rows spaced 35 cm, on grey-wooded soil. There were 70 cm between each plot consisting of 5 rows. Using a Latin square design, the rows were arranged into plots 175 × 300 cm with the following treatments: (1) check (no weeds removed); (2) all weeds except NLHB removed; (3) only NLHB removed; and (4) all weeds removed. All weeding was done by hand. In the fall of 1982, several NLHB plants bearing mature seeds were placed on the control and 'NLHB-only' plots to ensure the presence of plenty of seeds. Only the central 1 m^2, consisting of 3 rows 1 m long, were evaluated. The plots were clipped once in July and August. The clipped vegetation was separated into NLHB, other weeds, and alfalfa, dried for 24 h at 100°C and weighed.

Effect of Chemical Control of NLHB on the Yield of Creeping Red Fescue

Plots of 3.7 × 15 m in size, were established on a two-year old stand of creeping red fescue (*Festuca rubra* L. var. Boreal; Gramineae) near Dawson Creek, British Columbia. The stand, located on a clay loam soil, was heavily infested with NLHB. Fall treatments were applied on 16 October 1972, when the fescue regrowth was 7–10 cm in height and when the NLHB was mainly in the rosette stage. Spring treatments were applied on 12 May 1973 when the fescue was in the vegetative stage (7–10 cm in height). On this date, the flowering stems of the NLHB were just starting to elongate. All treatments were applied in 165 l/ha of liquid. Fall treatments were replicated five times; spring treatments were replicated three times. Precipitation was considerably above normal during the fall of 1972 but below normal during the 1973 growing season. Crop injury evaluations, weed counts and harvest were obtained on 19 June 1983.

NLHB as a Source of Pollen

Pollen was collected by means of pollen traps from 24 May to 13 July 1983 on sites near Arborfield, Saskatchewan. At each collection date, subsamples of 5 g were taken. The orange pollen pellets were separated from those of other colours and weighed. NLHB was observed to yield yellow pellets while dandelions were observed to yield orange pellets (Mr. D. Valleau, beekeeper, Aylsham, Saskatchewan, pers. comm.). From the orange pellets and from pellets of the other colours, slides were prepared using the method given by Adams and Morton (1972). On these slides, the proportion of pollen grains resembling NLHB and dandelion was determined out of 1000 grains. Pollen grains of these two species were counted together as Wodehouse (1965) has shown that they cannot be distinguished with certainty. Using these percentages and assuming that pollen grains of the various species have approximately the same density, the percent of NLHB–dandelion type of pollen was determined by weight for the orange and the assorted pellets.

Results and Discussion

Occurrence in Alfalfa-brome Hayland

In 1982 there was a mean of 14.5 seedlings/0.25 m^2, and in 1983, 6.2. In 1983, NLHB covered 2% and other weeds (including grasses) 48% of the area within the quadrats. The small area covered by NLHB combined with the fact that it is readily eaten by cattle, means that NLHB causes little loss in perennial mixed forage crops.

Biomass Sampling in Alfalfa

NLHB constituted an average of only 5.7% and alfalfa 89.7% of the total biomass in the 13 alfalfa fields sampled in 1982 (Table 1). In June and July 1983, the alfalfa content remained near the same level while the NLHB content declined. Thus, NLHB constituted only a small portion of the total biomass produced in the fields. The carotene content of NLHB was about 1.5 times higher, the crude protein content 1.5 times lower, and the crude fibre content of NLHB was about the same as that reported by Waddington *et al.* (1976) for alfalfa (Table 2). In Table 3, the protein content of alfalfa hay is calculated when mixed with various proportions of NLHB. A protein content of 19% is assumed for alfalfa (Waddington *et al.* 1976) and 12% for NLHB. The minimum required crude protein level of dehydrated alfalfa pellets is 17%. Therefore, the NLHB content would have to exceed 25% to lower the protein content to less than 17%.

Table 1. Dry weight of narrow-leaved hawk's-beard, *Crepis tectorum* L. (NLHB), other weeds, and alfalfa in alfalfa fields used in the dehydration industry in the Parkbelt region of Saskatchewan.

	Mean Dry Weight (g/m^2)			
Date of Sampling	NLHB	Other Weeds	Alfalfa	Total Biomass
vii.82	8.8	7.6	143.2	159.6
vi.83	1.6	16.4	131.2	149.2
vii.83	2.8	28.4	170.8	202.0

Table 2. Crude protein, crude fibre and carotene content of NLHB (narrow-leaved hawk's-beard, *Crepis tectorum* L.) collected at the time of harvest of alfalfa in July 1982 and July 1983 in the Choiceland, Arborfield and Tisdale districts of Saskatchewan. For comparison, the crude protein, crude fibre and carotene content of alfalfa is given, as reported by Waddington *et al.* (1976).

Species	Date Collected	Crude Protein Mean %[1]	Crude Fibre Mean %[1]	Carotene Mean mg/kg[1]
NLHB	vii.82[2]	13.5 (±1.8)	27.6 (±0.44)	288.2 (±29.9)
	vii.83[3]	11.7 (±0.5)	26.6 (±1.27)	197.6 (±3.8)
Alfalfa	Fall 1973	20.4	28.4	174
	Fall 1974	17.3	31.4	152

[1] Standard error of the mean in brackets.
[2] $n = 3$.
[3] $n = 6$.

Hand-weeded Plots of Alfalfa and NLHB

The number of NLHB plants was very low in all plots. Removal of NLHB and other weeds did not significantly increase the yield of alfalfa in July and August (Table 4). Quite dense NLHB occurred in an uncultivated strip, about 4 m wide, bordering the plots. Thus it is obvious that the alfalfa suppressed the NLHB.

Effect of Chemical Control of NLHB on the Yield of Creeping Red Fescue

Chemical treatment, especially if applied in fall, was very effective in reducing the number of NLHB plants (Table 5). Crop tolerance was excellent except when higher rates of a mixture of dicamba (3,6-dichloro-O-anisic acid), 2,4-D ([2,4-dichlorophenoxy] acetic acid) and mecoprop (2[(4-chloro-o-tolyl)oxy] propionic acid), and 2,4,5-T ([2,4,5-trichlorophenoxy] acetic acid) and MCPA ([(4-chloro-o-tolyl)oxy] acetic acid) were applied. Despite the effectiveness of the chemical treatments crop yields were not increased. This confirms results obtained by Waddington *et al.* (1976) who reported no consistent increase in the yield of alfalfa and significant reductions in carotene and xanthophylls and increases in crude fibre content after some of the chemical treatments. Therefore, NLHB seems to be a poor competitor.

Table 3. Crude protein content of alfalfa hay at various levels of infestation with NLHB (narrow-leaved hawk's beard, *Crepis tectorum* L.). The crude protein content of pure alfalfa is assumed to be 19% (Waddington *et al.* 1976) and that of NLHB 12%.

Percent NHLB in Alfalfa Hay	Percent Crude Protein in Alfalfa Hay
5	18.7
10	18.3
15	18.0
20	17.6
25	17.3

Table 4. Number of NLHB (narrow-leaved hawk's-beard, *Crepis tectorum* L.), dry weight of NLHB, other weeds and alfalfa in grams on plots near Melfort, Saskatchewan, in July and August 1983.[1]

Mean No. and Dry Weight	All Weeds $(\bar{x})^2$	All Weeds Except NLHB $\bar{x}$	NLHB Only $(\bar{x})$	No Weeds $\bar{x}$
		July		
No. of NLHB	6.3 (±2.7) *ab*	2.3 (±1.3) *ab*	10.0 (±2.6) *a*	0.8 (±0.5) *b*
Dry wt: NLHB	0.8 (±0.3) *b*	0.3 (±0.2) *b*	5.1 (±1.8) *a*	0.1 (±0) *b*
Dry wt: other weeds	18.6 (±5.2) *a*	23.6 (±9.5) *a*	2.5 (±1.1) *a*	1.1 (±0.6) *a*
Dry wt: alfalfa	299.0 (±42) *a*	289.0 (±25) *a*	382.1 (±47) *a*	396.2 (±50) *a*
		August		
No. of NLHB	0.8 (±0.5) *a*	1.3 (±1.3) *a*	0.5 (±0.3) *a*	0.8 (±0.8) *a*
Dry wt: NLHB	0 (±0) *a*	0 (±0) *a*	0 (±0) *a*	0.1 (±0.1) *a*
Dry wt: other weeds	1.1 (±0.3) *a*	1.4 (±0.7) *a*	0.4 (±0.2) *a*	0.1 (±0) *a*
Dry wt: alfalfa	81.4 (±10.9) *a*	102.2 (±8.0) *a*	103.9 (±14.3) *a*	103.5 (±10) *a*

[1] ANOVA — means followed by the same letter in each row are not significantly different at $P = 0.05$.
[2] Standard error of the mean is given in brackets.

NLHB as a Source of Pollen

In 1983 the proportion of NLHB–dandelion type of pollen rose to a peak of 57% during the period of 1–8 June in the orange pollen pellets. In the assorted pellets, which included the yellow ones, this type of pollen increased to a maximum of 3.4% during the period of 15–17 June. This pattern is similar to that observed by Murrell and Szabo (1981) in the Peace River region. At the end of the blooming period of dandelion in about the middle of June, the content of pollen resembling NLHB and dandelion declined sharply (Table 6). If NLHB would have filled the gap from the end of the dandelion blooming season to the main honey flow, then the percent of NLHB–dandelion type of grains should have increased in the assorted pollen, which contained the yellow pollen. But this was not the case. Therefore it seems that in 1983 NLHB did not provide a significant amount of pollen.

Table 5. Effect of chemical control of NLHB (narrow-leaved hawk's beard, *Crepis tectorum* L.) on yield of creeping red fescue, var. Boreal, near Dawson Creek, British Columbia.

Treatment	Rate kg/ha	Crop Tolerance (0–9)	NLHB[1]		Fescue Seed Yield[1] (g/m^2)
			Plants/m^2	Dry Weight (g/m^2)	
Fall-applied Treatments					
Check, weedy	—	9	168 *a*	48.7 *a*	76 *a*
2,4-DB ester	1.1	9	25 *d*	4.6 *c*	82 *a*
2,4-DB ester	1.4	9	20 *d*	3.4 *c*	81 *a*
2,4-DB ester	1.7	9	10 *d*	1.6 *c*	73 *a*
2,4-DB ester	0.6	9	34 *cd*	4.2 *c*	94 *a*
2,4-DB ester	1.1	9	15 *d*	2.6 *c*	81 *a*
2,4,5-T + MCPA	0.2 + 0.2	9	88 *bc*	20.6 *b*	75 *a*
2,4,5-T + MCPA	0.4 + 0.5	9	53 *bcd*	10.2 *b*	70 *a*
MCPB	1.1	9	52 *bcd*	15.7 *b*	83 *a*
MCPB	1.7	9	53 *bcd*	21.7 *b*	82 *a*
Dicamba + 2,4-D + mecoprop	0.06 + 0.18 + 0.04	9	91 *b*	13.6 *b*	80 *a*
Dicamba + 2,4-D + mecoprop	0.13 + 0.35 + 0.08	8.5	44 *bcd*	6.8 *b*	72 *a*
Spring-applied Treatments					
Check, weedy	—	9	69 *a*	31.5 *a*	71 *a*
2,4-DB ester	1.4	9	10 *b*	2.3 *b*	53 *b*
2,4-DB ester	1.1	8	19 *b*	3.1 *b*	39 *a*
Dicamba + 2,4-D + mecoprop	0.13 + 0.35 + 0.08	8	20 *b*	4.4 *b*	71 *a*
2,4,5-T + MCPA	0.36 + 0.48	8	40 *ab*	9.5 *b*	71 *a*

[1] Within each season of treatment, means followed by the same letter are not significantly different at $P = 0.5$.

Suitability as a Target for Biological Control

From the data we have collected so far, it appears NLHB does not cause significant crop losses in mixed perennial forage crops in Saskatchewan. The populations found in alfalfa used in the dehydration industry did not reduce yield nor the quality below the required minimum. However, according to observations by farmers and personnel involved in the alfalfa dehydration industry, NLHB populations fluctuate greatly from year to year. In 1982 and particularly in 1983, alfalfa was very vigorous and therefore was able to suppress NLHB. Any agronomic practices that would increase the vigour of alfalfa would therefore reduce NLHB.

NLHB spreads by seed. Copious amounts of seed are produced if the plant is not cut before maturity. Therefore, seed-feeding insects should be given preference in any biological control program. There should be large reservoirs of seed setting NLHB for seed-feeding insects that might be introduced from abroad so that they could build up high populations. In 1982 and 1983 by far most infestations were less than 10 m^2 in size and alfalfa was harvested before most of the NLHB started to bloom. There were no large reservoirs for insects to develop in the seed heads. Therefore, on the basis of the limited data collected in 1982 and 1983, it is concluded that a seed-feeding insect could not control the large fluctuations of this weed. A full-scale biological control project, whereby several insects such as a leaf-feeder, seed-feeder, and a gall insect would be introduced, seems too costly in relation to the losses caused by NLHB. However, observations in 1984 indicated that NLHB became much more prevalent again and additional data were collected which could not be included in this paper. Reliable assessment of the damage caused by a strongly fluctuating weed such as NLHB must be based on data collected in 3 to 5 years.

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Table 6. Content of pollen grains of the NLHB (narrow-leaved hawk's-beard, *Crepis tectorum* L.) and dandelion-type in pollen collected from 24 May to 13 July 1983 in the area of Arborfield, Saskatchewan.

Date Collected	Weight of Total Sample (g)	Percent of the NLHB–Dandelion Type Pollen in		
		Orange Pollen Pellets	All Other Pellets	Total Sample
24–28 May	186.6	0.1	0.4	0.5
30 May	207.6	2.8	0.1	2.9
31 May	182.2	7.3	0.8	8.1
1–8 June	119.8	56.7	0.6	57.4
8 June	224.7	24.4	3.3	27.6
15–17 June	202.7	25.5	3.4	8.9
27 June	164.0	15.3	1.3	16.6
3 July	278.8	1.2	0.2	1.4
10 July	167.0	0.0	0.1	0.1
13 July	119.5	0.0	0.2	0.5

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Prospects for Biological Control of Velvetleaf (*Abutilon theophrasti*)

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Abstract

Velvetleaf, an annual malvaceous plant, is thought to be native to the People's Republic of China (PRC). Its historical use as a fiber crop may date back to 2000 B.C. The fiber has been used for rope, cordage, bagging, coarse cloth, fishing nets, paper stock, and for caulking boats. Introduction into North America may have occurred in the 17th Century as colonists searched for fiber sources. Although a commercial failure in the new world, velvetleaf thrives today as a major weed of maize, soybeans, and cotton. Yearly control costs in the U.S.A. are estimated to exceed $343 million. Control by biological means may be a method that will reduce velvetleaf's negative impact on U.S.A. agriculture. Recent surveys in India indicate that biotic agents associated with the plant are causing some degree of stress to vegetative and reproductive tissues. Further studies are underway in India to elucidate specificity and efficacy of these biotic agents, and relationships between agent and weed. Additional surveys are needed to find other natural enemies of velvetleaf in the PRC and adjacent territories. At the completion of these surveys, prospects for biological control of velvetleaf can be properly evaluated.

Les Perspectives de la Lutte Biologique Contre l'*Abutilon theophrasti* ('Velvetleaf')

On croit que le 'velvetleaf' (feuille-veloutée) une plante malvacée annuelle, soit indigène de Chine (RPC). L'usage historique de cette plante, comme fibre de culture, pourrait remonter à 2000 avant J.C. La fibre a été utilisée dans la fabrication de cordes, cordages, toile à sac, filets de pêche, et pâte à papier, ainsi que pour le calfeutrage des bâteaux. L'introduction en Amérique du Nord pourrait remonter au 17ième époque, où les colons cherchaient des sources de fibre. Quoiqu'ayant fait échec commercialement au nouveau monde, le 'velvetleaf' prospère aujourd'hui comme mauvais herbe importante parmi le maïs, le soya et le coton. Aux États-Unis, la lutte annuelle coute, on estime, plus de $343 million. La lutte biologique contre le 'velvetleaf' pourrait réduire ses effets négatifs sur l'agriculture américaine. Des enquêtes récentes en Inde ont indiqué que des agents biotiques en association naturelle avec cette mauvaise herbe sont à l'origine de certains pressions sur les tissus végétatifs et reproductifs. D'autres études sont en cours en Inde pour élucider la spécificité et l'efficacité de ces agents biotiques et pour définir leurs relations avec la mauvaise herbe en question. D'atures enquêtes serraient nécessaire en Chine et dans les territorires voisins pour découvrir d'autres ennemis naturels du 'velvetleaf', à la suite desquelles on pourrait évaluer de façon plus sûre les perspectives de la lutte biologique contre le 'velvetleaf'.

Introduction

Abutilon theophrasti Medik. (Malvaceae), is commonly called velvetleaf in the United States. It has also been called buttonweed, butterprint, Indian mallow, abutilon hemp, and Chinese jute. The species was originally described from India in 1787 (Il'in 1949; Riedl 1976). Synonyms are: *Abutilon avicennae* Gaertn. [1791], *Sida abutilon* L. [1753], *Sida tiliaefolia* Fisch. [1808], *Abutilon abutilon* (Linn.) Huth. [1893], *Sida mollis* Pavolini [1908], *Abutilon molle sensa* Dunn [1911], and *Abutilon avaricennae* var. *genuina* Skvortzow [1930].

Velvetleaf is a cool temperate annual with a simple erect stem which may grow to 4 m (Fig. 1). The large alternate, long petiolate leaves are broadly ovate, deeply cordate, long acuminate, crenate, green on both sides, and velvety with a dense covering of stellate hairs. The pale yellow flowers have five petals which are slightly notched apically and the calyx is cleft to or just below the middle. The flowers are borne on both the main stem and short terminal branchlets in racemes or, in the case of large plants, in racemose-paniculate inflorescences. The seed pods contain 12–15 carpels, are densely covered with soft bristles, and are tipped by aristate recurved beaks. The pod is mostly black at maturity (Il'in 1949) (Fig. 1).

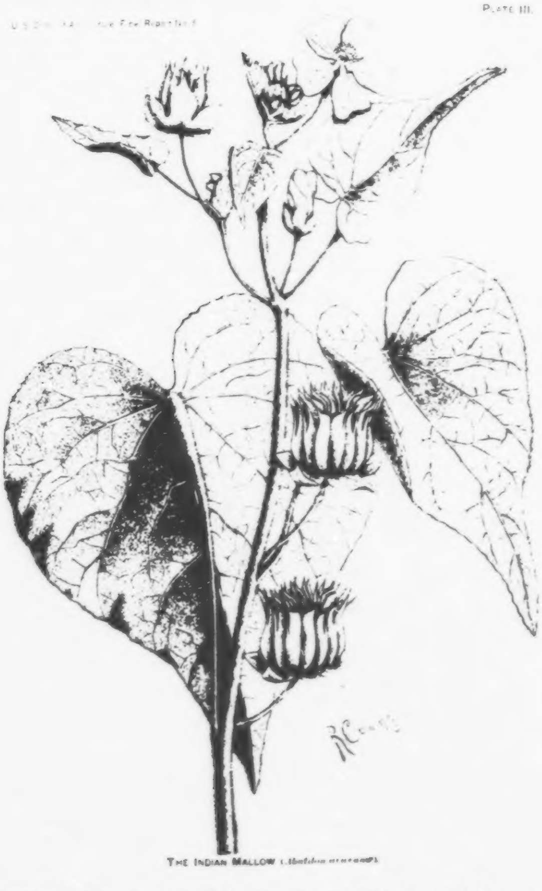

Fig. 1. *Abutilon theophrasti* Medik. from USDA fiber Report No. 6, 1894 (*A. avicennae* Gaertn. = *A. theophrasti*).

China is stated to be the origin of velvetleaf according to Vavilov (1951) and Li (1970). Locality records obtained from U.S., Asian, and European herbaria were used by the senior author to obtain an indication of the distribution of the plant in China. The majority of the collections had been made between latitude 30° N and 34° N in a band from the East China Sea to Northern Burma (Fig. 2).

According to Kirby (1963), velvetleaf is generally cultivated in China along with other crops, such as sorghum and winter wheat. The plants are harvested when in full flower and the whole plants are retted in water for the extraction of the fiber from the stem. Velvetleaf fiber grown in China and possibly Russia is used domestically and not exported. Prior to World War II, however, a considerable amount of this fiber was exported from China to Japan, Great Britain, and Germany (Dempsey 1957).

According to Hu (1955), the species is 'cosmopolitan in the temperate region of the northern hemisphere' and in China, *Abutilon theophrasti* var. *chinensis* (Skvortzow) with green stems is cultivated extensively while *A. theophrasti* var. *nigrum* (Skvortzow) with reddish-black stems is less common. In the USSR, *A. theophrasti* occurs as a weed of cotton, millet, and other crops and is usually found in the southern steppe and desert zones, in field margins, gardens, parks and river valleys (Il'in 1949).

The distribution of velvetleaf seed throughout the Northeast and North Central U.S.A. occurred as a result of the attempted use of the plant as a source of domestically grown fiber.

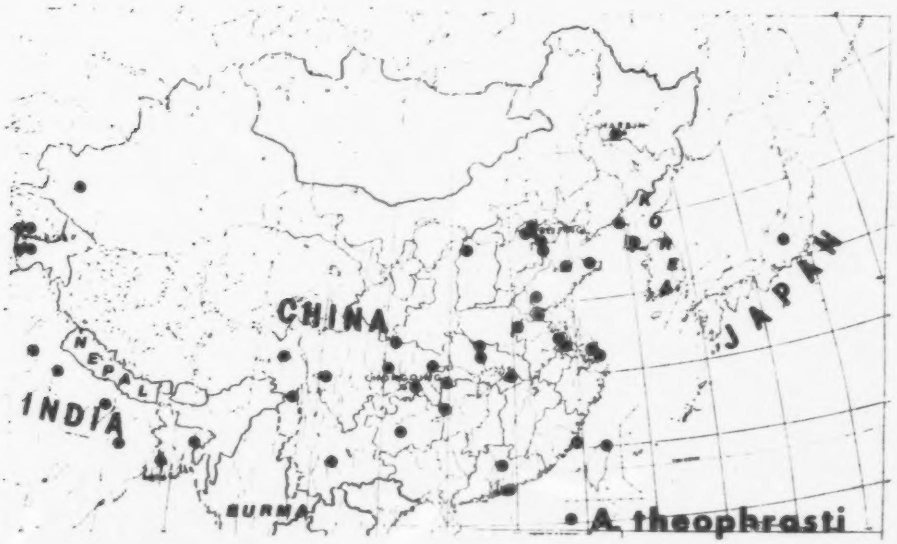

Fig. 2. Distribution of velvetleaf from India, through the People's Republic of China to Japan. Localities determined by herbaria records.

Velvetleaf was probably introduced into North America before 1700 as a potential source of fiber (Spencer 1984). Periodic attempts were made to establish velvetleaf as a fiber crop in the U.S.A. until 1972 (Dempsey 1975; Spencer 1984). These trials, over a period of *c.* 300 years, were unsuccessful and there are no records of velvetleaf as a commercial fiber crop in North America.

The plant appears well adapted to the temperatures, rainfall and soils of the major maize and soybean production areas of the U.S.A. Velvetleaf was estimated to be a weed problem in 33% of the maize and 38% of the soybean production land in 21 States of the midwestern U.S.A.; this weed was estimated to have cost farmers $343 million in control efforts in 1982 (Spencer 1984). Khedir and Roeth (1981) calculated that each velvetleaf plant in infested fields surveyed in Nebraska contributed *c.* 40 viable seeds to the seed population in the soil. Winter (1960) determined that undisturbed velvetleaf plants may produce 8000 seeds/plant. Inter- and intra-specific competition, seed predation, environmental factors and agronomic practices affect potential velvetleaf reproduction by limiting the number of viable seeds each plant contributes to the soil 'bank'. These seeds may remain viable for 20–50 years (Ewart 1908; Muenscher 1955).

Although we have information on the cost and extent of the problem in North America, we know very little about the weediness of velvetleaf in other areas where it has been introduced. Velvetleaf was reported to be found through the Middle East, North Africa, Europe, Scandinavia, and South America (Kirby 1963; Dempsey 1975; Spencer 1984). This distribution may be due to widely scattered attempts to use velvetleaf as a fiber crop.

Dempsey (1975) listed insects attacking *A. theophrasti* in different countries. These insect species are polyphagous, attacking cotton and other economic plants in and outside the family Malvaceae. Records of velvetleaf's insect enemies compiled by CIBC (1976) also showed them to be polyphagous with their host-plant range including economic plants.

Velvetleaf was one of several weeds targeted for biological control research in a joint PL-480 project between Dr. K.E. Frick, USDA/ARS, Stoneville, MS, and the CIBC Laboratory in Rawal Pindi, Pakistan. This project (#FG-PA-259) was conducted from 1975–80. Researchers in Pakistan found velvetleaf in low numbers in the Chitral Valley, north of Rawal Pindi and west of the Kashmir, India border.

On the request of N.R. Spencer and with funding from the International Research Division, Office of International Cooperation and Development, U.S. Department of Agriculture, Dr. Shashi B. Babbar searched books and periodicals in India for references to *A. theophrasti*. The following libraries were visited:

A. New Delhi
  1. Centre of Advanced Studies Library, Department of Botany, University of Delhi.
  2. Science Library, University of Delhi.
  3. Central Library, University of Delhi.
  4. Library, Indian Agricultural Research Institute.

B. Dehra Dun
  1. Central Library, Forest Research Institute and Colleges (FRI&C).
  2. The Library of Systematic Botany Branch, FRI&C.

C. Howrah
  1. Reference Library, Botanical Survey of India (BSI), Indian Botanic Garden.
  2. Central Library, BSI, Indian Botanic Garden.

D. Calcutta
  1. Library of the Industrial Section of BSI at Indian Museum.

E. Srinagar
  1. Library of Botany Department, Kashmir University.
  2. Central Library, Kashmir University.

A total of 564 botanical works were found and scanned for information on *A. theophrasti* (citations to earlier names were also examined). Of these, only 46 contained references to *A. theophrasti*. Dr. Babbar visited five herbaria and recorded the collection sites of *A. theophrasti* specimens. These herbaria were:

1. Herbarium of the Botanical Survey of India, Dehra Dun.
2. Herbarium of the FRI&C, Dehra Dun.
3. Central National Herbarium, BSI, Indian Botanic Garden, Howrah.
4. Herbarium of the Industrial Section of the BSI.
5. Herbarium of the Botany Department, University of Kashmir, Srinagar.

A total of 24 localities were identified as sites where *A. theophrasti* had been collected. Velvetleaf reported from localities such as Calcutta and Bombay may have been plants grown at botanical gardens. Chandrabose (1973) reported *A. theophrasti* from Coimbatore, the most southerly record for India. Fig. 2 shows the more northern sites in India and Pakistan, as well as the PRC, where *A. theophrasti* has been recorded. The 24 localities given for *A. theophrasti* are shown in Table 1.

Velvetleaf in India

Published records of *A. theophrasti* in India go back more than 200 years. Roxburgh (1832) described it as *Sida abutilon*, as 'a native of various parts of India, though not common'. He reported velvetleaf seed was received from Peking (*sic*) and cultivated in the (then) Bengal Province as a substitute for hemp and flax. The species was grown in the former East India Company's Botanical Garden, Calcutta, and in the Serampore Botanical Garden in the late 18th and early 19th centuries (Voigt 1844). Hooker (1875) included 12 species of *Abutilon* from India, naming *A. theophrasti* as *A. avicennae*, while Watt (1889) mentioned this species as one of the seven Indian *Abutilon* spp. of economic importance. The latter author believed it to be native to northwest India, Sind (now in Pakistan) and Kashmir, with its distribution extending to North Asia, South Europe, and North America. Until Chandrabose (1973) published a short note on velvetleaf's occurrence in Coimbatore, Tamil Nadu, where he had collected specimens in 1968, the species was only known from widely separated localities in Northern India, such as Gorakhpur in Eastern Uttar Pradesh (Kanjilal 1966), Daryapur in Haryana (Nair 1978), and Gulmarg in Jammu and Kashmir (Singh and Kachroo 1976). Prain (1903) remarked that *A. theophrasti* was somewhat rare in Bengal and Dacca (now in Bangladesh). The Central National Herbarium of the BSI, Howrah (Calcutta) has specimens from Khanpur in Rajasthan and Sambal in Jammu and Kashmir.

Table 1. Localities where *Abutilon theophrasti* Medik. was identified from literature references and herbaria references.

I. **India**
  A. Jammu and Kashmir
    1. Muzaffrabad Town
    2. Lower Kishen Valley
    3. Wular Lake
    4. Gulmarg
    5. Jhelum River
    6. Srinagar
    7. Sambar
  B. Haryana
    1. Daryapur, Hissar
    2. Karnal
  C. Uttar Pradesh
    1. West of Bijnaur
    2. Domakhand, Gorakhpur
  D. Rajasthan
    1. Aklera Road, Khanpur
  E. West Bengal
    1. Calcutta
  F. Maharashtra
    1. Bombay
  G. Tamil Nadu
    1. Valankulum, Coimbatore
II. **Pakistan**
    1. Rawalpindi
    2. Chitral
    3. Tartora (Khyber)
    4. Kurram
III. **Afghanistan**
    1. Guzar Bash
    2. Mazar-i-Sharif
    3. East Turkestan
    4. Kashghar
IV. **Bangladesh**
    1. Dacca

The only available reference to *A. theophrasti* (as *A. avicennae*) in Nepal is by Lancaster (1981). Surveys in Nepal by one of us (Sankaran) showed *A. theophrasti* was not found or even known there and that Lancaster (1981) had mistaken the widely cultivated and better known Indian jute *Corchorus* (Tiliaceae) for *A. theophrasti*.

The relative scarcity of *A. theophrasti* on the Indian subcontinent pointed to the need for surveys to locate the species wherever it occurs and to investigate possible causes for its rarity, particularly any natural enemies that keep velvetleaf's population reduced and scattered. On the basis of earlier distribution records, surveys were conducted by one of us (Sankaran) during 1983–84 in several areas of India, including Calcutta and Darjeeling (West Bengal), Coimbatore (Tamil Nadu), Dehra Dun, Gorakhpur and Varanasi (Uttar Pradesh), Khanpur (Rajasthan), Gulmarg and Srinagar (Jammu and Kashmir), Diphu, Gauhati, Jorhat, Lakhimpur and Sibsagar (Assam), Shillong (Meghalaya) and Itanager (Arunachal Pradesh). Botany Departments of the Universities in these areas were queried, including those in Gorakhpur, Jorhat, Kalyani, Shillong, Srinagar and Varanasi.

A. theophrasti was seen only in Coimbatore and in the area surrounding Srinagar. All the plants seen in the Kashmir Valley had green stems like *A. theophrasti* var. *chinensis*. Singh and Kachroo (1976) did not mention the presence of the species in Srinagar.

In Coimbatore, *A. theophrasti* was present in a small localized patch of wetland, which is part of a temporary lake, that remains flooded for over six months in the year. This land is used for growing vegetables, and the weed occurred as stray plants along the margin of vegetable plots.

Phenology of *Abutilon theophrasti* in the Kashmir Valley

Field observations during July–October 1983 provided information on the phenology of *A. theophrasti* in the Srinagar area of the Kashmir Valley. During a typical year, *A. theophrasti* will germinate in May or June; however, in 1983, germination had been delayed by a cool spring and the growing period was further shortened by snows in October. The first visit to Srinagar was made in early July 1983. A late spring with the minimum temperatures *c.* 12°C retarded plant growth. Most *Abutilon* plants were less than 25 cm high and in early vegetative growth although few were 38–45 cm high and had begun to flower. Cultivation of maize, grain legumes, and rice had started by this time.

During the second visit in early September, velvetleaf plants in many areas had reached their maximum vegetative growth (*c.* 150 cm), with large leaves, conspicuous flowers and fruit capsules. Some fruit capsules were mature and about to dehisce. In mid-October, plants in most areas visited were in final stages of their annual cycle. The majority of fruit capsules had shed their seed and leaves were turning yellow. Maize had been harvested and left-over *Abutilon* plants were very prominent in the fields. Rather early for the year, the Kashmir Valley experienced its first snowfall in October 1983.

Heavy snowfall during winter is common in the Kashmir Valley. After the onset of spring, when soil temperature and moisture levels become favourable, overwintering *A. theophrasti* seeds germinate. In the USSR flowering occurs during July–September and fruiting during August–October (Il'in 1949).

Insects Associated with Velvetleaf in India and Pakistan

The CIBC (PL-480 project #FG-PA-259) carried out a survey for natural enemies of several weeds including *Abutilon* in Pakistan during 1975–80. This survey covered nine species of *Abutilon*, including *A. theophrasti*. A large number of insects were recorded from other *Abutilon* spp. but only one species, *Atherigona orientalis* Schiner (Diptera: Muscidae) was reared from *A. theophrasti*. A stem gall-fly, *Hexomyza abutilonicaulis* Spencer (Diptera: Agromyzidae), recorded from other *Abutilon* spp., was shipped to the U.S.A. in 1979 for trial against *A. theophrasti*. It was reared with great difficulty on *A. theophrasti* in quarantine (USDA/ARS, Stoneville, MS, Res. Quarantine Facility) for no more than two generations when all the imported stock died (CIBC 1981; Frick and Quimby 1982). This gall-fly was not found on *A. theophrasti* in Pakistan.

One of the primary objectives of the surveys in India was to document the occurrence of *H. abutilonicaulis* on *A. theophrasti*. We have not found this stem gall-fly on velvetleaf in India.

A remarkable phenomenon noted even on small *A. theophrasti* plants was that the plants were able to discourage arthropod enemies by trapping the small, immature stages in the sticky glandular hair on the stem, leaf, and fruit capsules. The trapped organisms were observed dead and decomposing on the plants. The most common insect found thus immobilized was a *Haplothrips* sp. (Thysanoptera: Phlaeothripidae).

In the Kashmir Valley, the polyphagous *Heliothis armigera* Hübner (Lepidoptera: Noctuidae) was found to bore into immature and partially mature fruit capsules, but the level of damage inflicted by this insect was not significant. No *Heliothis* eggs were found on plants but young larvae were sometimes seen on the plants when flowers and fruit capsules started developing. Surprisingly, *Heliothis* was hardly ever noticed as a pest of maize in fields were the weed occurred almost as an intercrop.

In one area (Pattan) near Srinagar, some flower buds were found to have aborted and started wilting. At the slightest touch such flower buds dropped to the ground. Most of these buds did not show any insect or other organisms when they were dissected. A few buds yielded larvae of a midge, identified by Dr. K.M. Harris, Commonwealth Institute of Entomology, London, as *Clinodiplosis* sp. Dr. Harris has commented (pers. comm.) that the larvae of this widespread genus of midges are known to occur as secondary invaders in rotting plant tissues. Further collections and observations are necessary to identify the midge species and to understand its exact relationship with the flower buds and possible plant pathogens.

In another area near Srinagar, some *A. theophrasti* stems had lesions. The damage appeared as oval or irregular patches of decomposing stem tissue covered by soft brown cuticle, with a small hole located in the center. Efforts to find the causative agent are scheduled for the summer of 1984.

The following is a list of other insects collected on *A. theophrasti* in India and identified by CIE.

Coleoptera: Chrysomelidae
  Luperomorpha nigripennis Duv.
  Monolepta sp.
Homoptera: Cicadellidae
  Balclutha sp. ?*hortensis* Lindberg
  Macrosteles quadripunctulatus (Kirschbaum)
  M. sexnotatus (Fallen)
   (These two *Macrosteles* spp. are vectors of European aster-yellows.)
  Psammotettix striatus (L.)
   (Vector of winter wheat mosiac.)
Psylloidea: Aphalaridae
  Aphalara maculipennis Low
Heteroptera: Lygaeidae
  Oxycarenus laetus Kirby

Large numbers of *L. nigripennis* and *Monolepta* sp. were seen on leaves of *A. theophrasti* and on the leaves and ears of maize plants in September but no damage was noticed. These chrysomelids apparently breed on one or more other weeds in the same area. Leafhoppers were numerous and observed only at the end of the crop season (October) in one area (Hajjan) where the *Abutilon* plants were senescent and interspersed with other wild, low-lying vegetation. *O. laetus*, a pest of cotton, was the only insect attacking the plant at Coimbatore, where it severely impaired seed production and viability.

Diseases of Velvetleaf

Nothing is known of the diseases of *A. theophrasti* in India but a complex of fungal pathogens and at least three different viruses have been reported from other countries (Dempsey 1975). Almost all these are known to infect cultivated plants. Diseases of *A. theophrasti* have received special attention in areas where the plant is cultivated for fiber. Becerescu (1979) published a handbook for control of diseases of velvetleaf and other fiber plants in Europe. In Illinois, where velvetleaf is a common weed in soybean fields, it serves as a wild host for three species of fungal pathogens of soybean (Hepperly *et al.* 1980).

A search for other pathogens infecting the plant in its wild state and in restricted habitats might determine if there are any that are host-specific and have potential as biocontrol agents.

Discussion

Velvetleaf merits further exploratory surveys for natural enemies in its native distribution range, and more detailed studies on the promising species. The recent surveys in the Indian subcontinent have only covered some of the areas along the periphery of the weed's native range, with the center of origin presumably somewhere in the PRC. The previous records of insects and plant pathogens attacking *A. theophrasti* are almost entirely from territories where the species has been introduced and cultivated for some centuries. Further surveys should extend to the PRC and areas immediately adjacent to it. Accessibility to these areas and facilities for field and laboratory studies are now limited, but should improve with more contacts with administrative agencies and collaboration with scientific institutions in the PRC.

From the available evidence it seems unlikely that velvetleaf originated in the Indian subcontinent. The virtual absence of this species in a wild state in the areas surveyed and the small number of species of insects associated with it would support this conclusion. The dusky cotton bug, *O. laetus*, found infesting the mature fruit capsules at Coimbatore, a cotton-growing area, may be limiting the spread of the weed.

While the stem gall-fly *H. abutilonicaulis* has been recorded from other *Abutilon* spp. in India and Pakistan, it has not been found to attack *A. theophrasti*. Of the seven susceptible *Abutilon* species occurring in Pakistan, three are highly susceptible and four show low susceptibility (CIBC 1979). Since the susceptible species also occur in India, *H. abutilonicaulis* may have co-evolved with them over time. The lack of susceptibility of *A. theophrasti* may indicate it is an alien species or that it has developed resistance to *H. abutilonicaulis*. *A. theophrasti* thrives in the Kashmir Valley like an introduced, agressive weed. The organism causing wilted flower buds and another unknown organism causing stem lesions in Kashmir are biotic factors that warrant further investigation.

Studies underway in Srinagar in 1984 and beyond, are combining the disciplines of entomology and plant pathology. This team approach may assist us in the evaluation of the potential for finding biocontrol agents in India.

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Chapter Three
Plant and Agent Variability

Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., p. 179 (1985)

Organisms as Taxonomists or the Contribution of Vascular Plant Taxonomy and Biosystematics to Biological Control

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Abstract

It is rarely appreciated that all taxonomic treatments are basically special purpose taxonomies; that is, that they utilize a limited number of characters whose nature best serves the purpose for which the classification is intended. The needs of botanists with respect to classification have changed dramatically in the last seventy-five years. A brief historical review is given to illustrate why many classical taxonomic treatments are unsuited to the requirements of biological control research. The needs of such programs are evaluated, and the potential contribution of biosystematics studies to biological control is discussed.

Les Organismes Comme Taxonomistes — ou les Contributions de la Taxonomie des Plantes Vasculaires et de la Biosystématique à la Lutte Biologique

On n'apprécie que rarement que tous les traitments taxonomiques sont essentiellement des taxonomies spécifiques; c'est à dire qu'elles se basent sur un nombre restreint de caractères dont la nature conforme le mieux au but prévu de la classification. Les besoins des botanistes en matière de classification ont changé de façon drammatique, durant les dernières soixante-quinze années. Un bref historique est destiné à éclaircir pourquoi beaucoup de traitements taxonomiques classiques ne se prêtent pas aux besoins de la recherche en matière de lutte biologique. On évalue les besoins de ces programmes et on analyse la contribution potentielle de la biosystematique à la lutte biologique.

Proc. VI Int. Symp. Biol. Contr. Weeds, 19–25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 181–9 (1985)

Ethological and Genetic Differences Among Three Biotypes of *Rhinocyllus conicus* (Coleoptera: Curculionidae) Introduced into North America for the Biological Control of Asteraceous Thistles

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Abstract

In replicated field trials, the Italian thistle biotype of *Rhinocyllus conicus* clearly was better at colonizing Italian thistle, *Carduus pycnocephalus*, than milk thistle, *Silybum marianum*, in southern California. The Italian thistle biotype was much less predisposed to oviposit on milk thistle heads than the milk thistle biotype was predisposed to oviposit on Italian thistle heads. Milk thistle flower heads did not support larval development by the Italian thistle biotype, even when, after 6 to 10 years and having reached 'explosive' population densities, weevils belonging to this biotype finally began ovipositing on nearby milk thistle capitula. In contrast, the milk thistle biotype quickly, successfully, and year-by-year increasingly, transferred to Italian thistle heads under field conditions.

Six polymorphic loci were assayed using starch gel electrophoresis to examine possible genetic differences among the Italian, milk, and musk thistle (*C. nutans*) biotypes of *R. conicus*. Only one locus showed a fixed genetic difference, but significant differences in allelic frequencies at four of the other five loci supported the biotype designation for the three, representative, weevil populations assayed.

Des Differences Éthologiques et Génétiques parmi Trois Biotypes de *Rhinocyllus conicus* (Coleoptera: Curculionidae) Introduites en Amérique du Nord dans la Lutte Biologique Contre des Chardons Asteracés

Dans des essais parallèles sur le terrain, en Californie du Sud, le biotype 'chardon italien' de *Rhinocyllus conicus* colonisait nettement mieux le chardon italien, *Carduus pycnocephalus* que du chardon-Marie, *Silybum marianum*. Le biotype 'chardon italien' était bien moins prédisposé à pondre sur les fleurons du chardon-Marie que n'était le biotype 'chardon-Marie' sur les fleurons du 'chardon italien'. Les fleurons du chardon au lait ne soutenaient pas les larves du biotype 'chardon italien', même lorsque, après avoir atteint des densités 'explosives' de population, en 6 à 10 années, des charançons de ce biotype commencaient enfin à pondre sur ces fleurons. Par contre, le biotype 'chardon-Marie' s'adaptait avec succès et chaque année davantage aux fluerons du chardon italien, en milieu ouvert.

On a essayé six loci polymorphes, au moyen d'éléctrophorèse à gel d'amidon, pour examiner des differences génétiques possibles, parmi les biotypes des chardons 'italien', chardon-Marie et au chardon penché (*C. nutans*). Une difference génétique fixe se presentait chez un seulement des six loci examinés, mais chez quatre des cinq autres des differences significatives de fréquence allélique sont venues appuyer les désignations de biotype retenues pour les trois populations representatives de charançons essayées.

Introduction

Goeden (1978) reported differences in the attack behavior and performance of *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae) as a biological control agent

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of Italian thistle, *Carduus pycnocephalus* L. (Compositae), versus milk thistle, *Silybum marianum* (L.) Gaertner (Compositae), in southern California. He suggested that weevils collected from these two thistles in different parts of Italy and colonized separately on the same thistles in southern California belonged to different, conspecific 'races' or 'strains', *sensu* Zwölfer (1967) and Zwölfer *et al.* (1971). A third 'biotype', *sensu* Gonzales *et al.* (1979), originating in France on musk thistle, *C. nutans* L., was thought to complete this subspecific triad of imported natural enemies. This last biotype is now widely established on musk thistle in Canada (Harris and Zwölfer 1971) and the United States (Schröder 1980; Trumble and Kok 1982). Recently, Zwölfer and Preiss (1983) confirmed the existence of these three biotypes ('ecotypes') in western Europe and identified several others which also showed marked differences in their host selection and oviposition behaviour. This paper describes field and laboratory studies conducted in southern California on the three biotypes of *R. conicus* introduced into North America.

Materials and Methods

Colonization Efficiencies of Imported Biotypes of R. conicus

Goeden (1978) suggested that the earliest attempt to establish *R. conicus* on milk thistle in northern California failed because the weevil biotype and weed species were mismatched; i.e. weevils from musk thistle did not colonize milk thistle (Hawkes *et al.* 1972). A field test of the need to match weevil biotype and appropriate thistle species during colonization was conducted in 1978 and 1979 during our last major effort to redistribute weevils throughout the known ranges of Italian and milk thistles in southern California (Goeden and Ricker 1977, 1978).

Eight well-separated colonization sites bearing isolated populations of milk thistles, but no *R. conicus*, were located. Similarly, eight colonization sites with Italian thistles, but no *R. conicus*, were located. During late March and early April 1978 and 1979, overwintered weevils were collected from rosettes of Italian thistle at the initial colonization site for this weevil biotype at See Canyon, San Luis Obispo County (Goeden and Ricker 1978). Five hundred vigorous weevils were released at each of the 16 locations within 2 days after their collection or after 2 or 3 days of laboratory storage at 2°C. The number of weevils colonized at each site was much greater than the minimum number of weevils usually needed to start a colony with spring releases (Kok 1974; Goeden and Ricker 1977, 1978). One or two years later, during peak flowering, each colonization site was closely examined for weevils and for eggs affixed to capitula as evidence of the survival and reproduction of *R. conicus.*

Ovipositional Preferences of Imported Biotypes of R. conicus

Goeden (1978) reported ovipositional preferences expressed in the field by the biotypes of *R. conicus* derived from milk thistle and Italian thistle for the same thistles from which they were collected in Italy. However, he also noted that weevils derived from milk thistle showed a less absolute preference and oviposited to a limited extent on Italian thistles growing intermixed with milk thistles at two initial colonization sites. We continued to monitor the ovipositional preferences of each weevil biotype beyond 1976, the last year reported by Goeden (1978), at two locations where both species of thistle are present. One location was the original release site in See Canyon for weevils imported from Italian thistle in southeastern Italy in 1973 (Goeden and Ricker 1978). The other location was at Lake Casitas, Ventura County, where weevils originating on milk thistle near Rome, Italy, were colonized on this same weed in 1972 (Goeden and Ricker 1977). During annual surveys at each location, eggs laid on capitula of milk thistle and Italian thistle were recorded during the peak oviposition period of *R. conicus*.

Genetic Differences Among Imported Biotypes of R. conicus

Thanks to Dr. Loke T. Kok, Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, 304 live weevils collected from musk thistle in Virginia were received at Riverside on 15 May 1980. Upon arrival, these weevils were killed and stored in liquid nitrogen for future analysis by starch gel electrophoresis. Similarly, 320 live weevils of the milk thistle biotype aspirated from bolting milk thistles at Goleta, Santa Barbara County, on 1 April 1980, were stored in liquid nitrogen, as were 325 live weevils collected from Italian thistle rosettes in See Canyon on 1 April 1980.

In mid-1982, starch gel electrophoresis employing standard techniques (Selander *et al.* 1971; Bush and Heuttel 1972) was used to assay the three biotypes of *R. conicus*. Bridge and gel buffers were prepared as tris citrate III, modified from Selander *et al.* (1971) (bridge, 0.57 M Tris, 0.157 M citrate [monohydrate], 0.001 M EDTA, pH 7.7; gel, 0.0248 M Tris, 0.0055 M citrate, 0.5 mM EDTA, pH 7.7). Weevils were individually homogenized in 25 μl of 0.1 M Tris-HCL. This provided enough homogenate to saturate two, 3 × 12 mm, filter paper wicks (Whatman #1) which were loaded into different gels.

A preliminary survey of the following 16 enzyme systems was conducted to locate polymorphic loci: aconitase (ACON), peroxidase (PER), diaphorase (DIA), esterase (EST), frutose 1,6-diphosphatase (Fl,6), fumerase (FUM), glucose 6-phosphate dehydrogenase (G6P), glutamate-oxaloacetate transaminase (GOT), α-glycerolphosphate dehydrogenase (aGPD), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), leucine animopepsidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), 6-phosphogluconate dehydrogenase (6PGD), and phosphoglucomutase (PGM). Of the 12 loci found to be polymorphic, six (Fl,6, GOT, IDH-l, IDH-2, ME and PGM) were of sufficient quality and reliability to assay the three weevil populations.

Results and Discussion

Weevils derived from Italian thistle clearly were superior for establishing colonies on Italian thistle compared to milk thistle (Table 1). After 1 or 2 years, adults and eggs of *R. conicus* were present, and establishment presumed successful, at seven of eight release sites on Italian thistle, but no establishment occurred at the eight release sites with milk thistle. The small numbers of eggs found on seven flower heads at Diamond Bar and five heads at Rowland Heights probably were laid by a few immigrants from one or both of the two nearest colonies of milk thistle-derived *R. conicus* established on milk thistle since 1972 and 1976 at distances of 2.4 and 1.3 km, respectively. These few batches of eggs better reflected oviposition resulting from limited weevil immigration into these insufficiently isolated, 1979 colonization sites, rather than clumped oviposition radiating outward from release points by newly established weevil colonies 1 or 2 years after their initial release (Goeden 1978; Zwölfer and Preiss 1983).

The above results supported the assertion by Goeden (1978) that mismatched weevil biotype and weed species probably were responsible for the initial failure to establish *R. conicus* on milk thistle in northern California (Hawkes *et al.* 1972). Similar mismatches are suggested by apparent failures of weevils collected from *Carduus personata* (L.) Jaquin and *Cirsium* spp. (Compositae) in Europe to colonies plumeless thistle, *Carduus acanthoides* L., in Canada (Harris 1984). Zwölfer and Preiss (1983) recommended the future use of biotypes of *R. conicus* appropriate to the target weeds of concern; e.g. the biotype associated with *Cirsium vulgare* (Savi) Tenore, not the biotype from *Carduus nutans*, should *R. conicus* be introduced from Europe for the biological control of *C. vulgare*. They also recognized separate European biotypes of *R. conicus* associated with musk thistle, milk thistle, as well as the two, small-headed thistles, Italian thistle, and slenderflower thistle (*Carduus tenuiflorus* Curt.). These field results and recommendations with *R. conicus* seemingly contradict the notion that oligophagous natural enemies are better biological control agents than monophages, based on the assumption that the former inherently are more trophically disruptive; i.e. possess less 'ecological homeostasis', especially if obtained from hosts other than the target weed (Pimental 1963; Harris 1973; but also see Room 1981 and Goeden 1983).

Table 1. Results of colonization of 500 *Rhinocyllus conicus* Froelich weevils collected from Italian thistles at See Canyon, San Luis Obispo County, in March and April, 1978 and 1979, at each of 16 locations on milk or Italian thistles in southern California.

Thistles on which colonized	Where colonized	When colonized	*R. conicus* present in 1979 or 1980?
Milk	Foster Park, Ventura Co.	27.iv.1978	No
"	Newhall, Los Angeles Co.	12.v.1978	No
"	Morretti Canyon, San Luis Obispo Co.	4.iv.1979	No
"	Nipomo, San Luis Obispo Co.	4.iv.1979	No
"	Buellton, Santa Barbara Co.	5.iv.1979	No
"	Brea, Orange Co.	5.iv.1979	No
"	Diamond Bar, Los Angeles Co.	5.iv.1979	Yes[1]
"	Rowland Heights, Los Angeles Co.	5.iv.1979	Yes[2]
Italian	Bonita, San Diego Co.	31.iii.1978	No
"	Sunnyside, San Diego Co.	31.iii.1978	Yes
"	Buellton, Santa Barbara Co.	7.iv.1978	Yes
"	Lake Cachuma, Ventura Co.	7.iv.1978	Yes
"	Las Flores Canyon, Santa Barbara Co.	13.iv.1978	Yes
"	Dos Pueblos Canyon, Santa Barbara Co.	13.iv.1978	Yes
"	El Cajon, San Diego Co.	17.iv.1978	Yes
"	La Mesa, San Diego Co.	17.iv.1978	Yes

[1] Two adults and 90 eggs were found on 7 of 150 flower heads in 1980.

[2] Eleven eggs were found on 5 of 200 flower heads in 1980.

Significantly, and somewhat surprisingly, Jessup (1981) reported the successful colonization of *R. conicus* derived from musk thistle in Canada on musk thistle, Italian thistle, plumeless thistle, and slenderflower thistle in New Zealand. He stated that all four *Carduus* spp. were acceptable hosts of *R. conicus* in New Zealand. This seems to contradict the report by Zwölfer and Preiss (1983) that Italian and slenderflower thistles were not attacked by *R. conicus* in most localities they sampled in southern and western France, where the musk thistle biotype also occurred. Jessup (1981) noted that only 8% of the *R. conicus* survived from eggs to adults in heads of Italian and slenderflower thistles in New Zealand, and he attributed this mortality to intraspecific competition for food by excess larvae which completely destroyed the small heads before most individuals completed development. In fairness, we note that Jessup now acknowledges differences in the host suitability of these four thistles for *R. conicus* (Harris, pers. comm. 1983). Rees (1978), on the other hand, attributed the high larval mortality he found in capitula of native and introduced *Cirsium* thistles attacked by the musk thistle biotype of *R. conicus* in Montana, U.S.A., to the 'marginal suitability' of these hosts, because most larvae died as early instars from no obvious cause. Goeden and Ricker (1980) reported similar, otherwise unattributable, larval mortality in the large heads of milk thistle in southern California. New Zealand might still benefit by introducing the Italian thistle biotype of *R. conicus*, which supposedly is better adapted to Italian thistle as well as slenderflower thistle (Zwölfer and Preiss 1983); although our unpublished field data suggest differences in the performance of the biotype even on these two closely related thistles.

Table 2. Incidence of *Rhinocyllus conicus* Froelich (Italian thistle biotype) eggs on Italian thistle versus milk thistle capitula recorded during annual field surveys in See Canyon, California, during 1973–83.

Year	Italian Thistle				Milk Thistle			
	Flower Heads Examined		Eggs Recorded		Flower Heads Examined		Eggs Recorded	
	Total No.	No. with eggs (%)	Total No.	$\bar{x}$/infested head	Total No.	No. with eggs (%)	Total No.	$\bar{x}$/infested head
1973	2693	80 (2.9)	115	1.4	163	0 (0)	0	0
1974	3156	42 (1.3)	60	1.4	107	0 (0)	0	0
1975	3340	111 (3.3)	210	1.9	41	0 (0)	0	0
1976	1879	125 (6.7)	272	2.2	—	— —	—	—
1977	561	509 (90.7)	1716	3.4	100+	0 (0)	0	0
1978	653	587 (90.7)	2263	3.9	300	9 (3.0)	57	6.3
1979	543	534 (98.3)	2961	5.5	115	27 (23.5)	159	5.9
1980	523	523 (100)	3305	6.3	162	92 (56.8)	573	6.2
1981	632	632 (100)	3560	5.6	199	29 (14.6)	111	3.8
1982	637	623 (100)	3026	4.9	139	110 (79.1)	739	6.7
1983	606	604 (99.7)	3971	6.6	190	105 (55.3)	630	6.0

The ovipositional preferences of the Italian thistle and milk thistle biotypes for heads of Italian and milk thistles were markedly different under field conditions and have changed during the past decade (Tables 2 and 3). The Italian thistle biotype of *R. conicus* first oviposited on milk thistle at See Canyon 6 years after initial colonization when oviposition on flower heads of Italian thistle approached saturation (Table 2). In contrast, the milk thistle biotype began ovipositing on Italian thistle only 1 year after its colonization on milk thistle at Lake Casitas, and slowly and steadily increased its rate of oviposition over the next decade until nearly half of the Italian thistle heads received eggs (Table 3). This indicated that the ovipositional preferences of these two biotypes were not rigidly fixed, were capable of changing within a relatively short period of time, and appeared to be influenced to different degrees by weevil densities. The Italian thistle biotype was much less predisposed to oviposit on milk thistle than the milk thistle biotype was predisposed to oviposit on Italian thistle heads.

Ovipositional preferences imperfectly reflected behavioral differences between the milk thistle and Italian thistle biotypes. From the early onset of oviposition on Italian thistle capitula at Lake Casitas (Table 3), the eggs of the milk thistle biotype readily developed to adults. So far, however, none of the eggs laid on the heads of milk thistle by the Italian thistle biotype in See Canyon (Table 2) has been found to develop beyond the first instar. Harris (1984) suggested that larval mortality in the heads of marginal hosts may result from receptacle tissue proliferation at the site of larval feeding which crushes the larvae. This was not the case with the Italian thistle biotype on milk thistle capitula in southern California. Our dissections indicated instead that newly hatched larvae failed to exit from the large, outer bracts (phyllaries) of the milk thistle capitula upon which the eggs hatched. The first instars usually mined towards the base of the bracts and died, apparently unable either to pass through the basally constricted point of attachment or to chew laterally from the outer bract into the underlying bracts and receptacle. The small heads of Italian thistle, on the other hand, with their thin, closely appressed involucral bracts presented no such barrier to the first instars of the milk thistle biotype. These observations indicate that the number of eggs oviposited in nature on the flower heads of a particular species of thistle may not be an accurate index of its suitability as a host plant for *R. conicus* (Jessup 1981; Zwölfer and Preiss 1983; Harris 1984, Table 2).

Table 4 summarizes the results of the electrophoresis. Two alleles were observed at the Fl,6 locus. The Italian thistle and milk thistle biotypes were polymorphic at this locus, whereas the musk thistle biotype was fixed for the faster migrating allele (Fl,6^{100}). However, although the Italian thistle and milk thistle biotypes of *R. conicus* shared both alleles, the frequencies were significantly different ($\chi^2 = 110$, $P < 0.001$). Both populations were in Hardy-Weinberg equilibrium.

Table 3. Incidence of *Rhinocyllus conicus* Froelich (milk thistle biotype) eggs on milk thistle versus Italian thistle capitula recorded during annual field surveys at Lake Casitas, California, during 1973–83.

	Milk Thistle				Italian Thistle			
	Flower Heads Examined		Eggs Recorded		Flower Heads Examined		Eggs Recorded	
Year	Total No.	No. with eggs (%)	Total No.	$\bar{x}$/infested head	Total No.	No. with eggs (%)	Total No.	$\bar{x}$/infested head
1973	397	126 (31.7)	623	4.9	1119	1 (0.1)	1	1
1974	342	165 (48.3)	900	5.5	1254	5 (0.3)	5	1
1975	278	261 (93.9)	2672	10.2	—	— —	—	—
1976	237	227 (95.8)	3155	13.9	1246	37 (3.0)	56	1.5
1977	122	121 (99.2)	1007	8.3	1036	17 (1.6)	—	—
1978	223	223 (100)	5363	24.1	884	117 (13.2)	172	1.5
1979	130	130 (100)	7064	54.3	634	207 (32.4)	371	1.8
1980	128	128 (100)	4981	38.9	531	237 (44.6)	486	2.1
1981	113	113 (100)	5887	52.1	622	219 (35.2)	434	2.0
1983	207	207 (100)	6586	31.8	607	290 (47.8)	658	2.3

Four alleles were found at the GOT locus, but two (GOT^{112} and GOT^{144}) were rare. Both the Italian thistle and milk thistle biotypes were polymorphic for GOT^{69} and GOT^{110}, with the milk thistle biotype also containing GOT^{112}. All three weevil populations were at Hardy-Weinberg equilibrium. The differences in allelic frequencies between the milk thistle and Italian thistle biotype were significant ($\chi^2 = 9.89$, $P < 0.01$, all rare alleles pooled).

Two IDH loci were observed in the weevils. At the fast locus (IDH-1), the Italian thistle and musk thistle biotypes (both from *Carduus* spp.) were monomorphic for IDH-1^{100}. The Italian thistle biotype contained an uncommon allele (IDH-1^{56}), but the three populations did not differ significantly in the frequency of IDH-1^{100} ($\chi^2 = 3.84$, $P < 0.05$). The slow locus (IDH-2) showed a fixed difference among the biotypes. The musk thistle biotype was fixed for a unique allele (IDH-2^{86}), while the Italian thistle biotype was fixed for IDH-2^{100}. The milk thistle biotype, possibly derived from the Italian thistle biotype, also contained IDH-2^{100}, but only at a frequency of 0.36.

Three alleles were observed at the ME locus, one of which (ME^{115}) occurred only in the musk thistle biotype. This biotype also deviated significantly from Hardy-Weinberg equilibrium. However, this was the only significant case out of the 12 tests, and generally

Table 4. Summary of electrophoresis of three *Rhinocyllus conicus* Froelich weevil populations as six loci ($n=50$).

Locus	Zygotic Frequency				Allelic Frequency (±SE)				χ^2[1]
Fl,6	50/50	50/100	100/100		50	100			
ex. milk thistle	0.28	0.54	0.18		0.55±.07	0.45±.07			0.33 ns
ex. Italian thistle	0	0.02	0.98		0.01±.01	0.99±.01			0 ns
ex. musk thistle	0	0	1.00		0	1.00			—
GOT	69/100	100/100	112/112	100/144	69	100	112	144	
ex. milk thistle	0.14	0.84	0.02	0	0.07±.03	0.91±.03	0.02±.2	0	0.75 ns
ex. Italian thistle	0.02	0.98	0	0	0.01±.01	0.99±.01	0		0 ns
ex. musk thistle	0	0.96	0	0.04	0	0.98±.02	0	0.02±.02	0.05 ns
IDH-1	56/100	100/100			56	100			
ex. milk thistle	0	1.00			0	1.00			—
ex. Italian thistle	0.04	0.96			0.04±.03	0.96±.03			1.71 ns
ex. musk thistle	0	1.00			0	1.00			—
IDH-2	86/86	100/100	100/171	171/171	86	100	171		
ex. milk thistle	0	0.08	0.56	0.36	0	0.36±.07	0.64±.07		2.35 ns
ex. Italian thistle	0	1.00	0	0	0	1.00	0		—
ex. musk thistle	1.00	0	0	0	1.00	0	0		—
ME	100/100	100/109	109/109	115/115	100	109	115		
ex. milk thistle	0.40	0.46	0.14	0	0.63±.07	0.37±.07	0		0 ns
ex. Italian thistle	0.80	0.18	0.02	0	0.89±.04	0.11±.04	0		0.01 ns
ex. musk thistle	0.60	0.22	0.16	0.02	0.71±.07	0.27±.07	0.02±.02		9.39 $P<0.01$
PGM	88/100	100/100	100/112	112/112	88	100	112		
ex. milk thistle	0	0.22	0.44	0.34	0	0.44±.07	0.56±.07		0.55 ns
ex. Italian thistle	0	1.00	0	0	0	1.00	0		—
ex. musk thistle	0.02	0.90	0.08	0	0.01±.01	0.95±.03	0.04±.03		0.01 ns

[1] Test for Hardy-Weinberg equilibrium.

is about what would be expected by chance alone. All three biotypes shared the two common alleles, although the frequencies were significantly different ($\chi^2 = 18.58$, $P < 0.01$).

Locus PGM also contained three alleles, with PGM^{88} being rare. The Italian thistle biotype was fixed for PGM^{100}. This allele was also the major allele in the musk thistle biotype. Both polymorphic populations (biotypes) were at Hardy-Weinberg equilibrium.

The three populations of weevils tested clearly are closely related genetically. Only one of the six loci (IDH-2) showed a fixed difference. All other loci shared common alleles and the only differences were in the frequencies. However, significant differences among the weevil populations assayed at five of the six polymorphic loci support the biotype designation based on ethological differences. The two biotypes associated with *Carduus* spp. differed at only a single locus (IDH-1), although the musk thistle sample originated in Virginia and the Italian thistle weevils were from California. Conversely, the Italian thistle and milk thistle biotypes differed at three loci (F1,6, GOT, and PGM), although both populations were from southern California. This indicated that the genetic differences among these biotypes probably existed in the parental European populations and did not arise subsequent to the introductions of these weevils into North America.

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Rates of Change in Introduced Organisms

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Abstract

Biological control workers have long been familiar with arguments concerning the importance, or lack thereof, of genetic variation in the successful establishment of a weed or a biocontrol agent. However, theories that deal with the genetic events accompanying the introduction of organisms have developed substantially in recent years. In particular, there have been studies of both natural and experimental examples of the interactions between chance events and the genetic systems determining characters that are selected for the new environment. These have led to clearer ideas of the nature of genetic 'transiliences', and the circumstances under which they are most likely to occur. Here I review the evidence from my own work and from the literature on the extent to which these circumstances have accompanied successful introductions of biocontrol agents. Probable cases are pointed out, and implications for rearing and release strategies are outlined.

Vitesses de Mutation Chez les Organismes Introduits

Les responsables de la lutte biologique connaissaient depuis longtemps les raisonnements concernant l'importance, ou le manque d'importance de variations génétiques lorsqu'il s'agit de l'établissement d'une mauvaise herbe ou d'un agent de lutte biologique. Cependent, on a developé d'une manière significative, avec les années récentes, les théories à propos des événements génétiques qui accompagnent l'introduction d'organismes. En particulier, on a étudié des exemples naturels et experimentaux des interactions entre des événements produit par le hasard et les systemes génétiques qui determinent les caractères appropriés aux environnements nouveaux. Ces études ont clarifié la nature de 'transiliances' génétiques et des circonstances les plus susceptibles de les produire. Ici on passe en revue les observations, tiré de mon travail et de la litterature, concernant le dégré auquel ces circonstances ont accompagné les cas d'introduction reussie d'agents de lutte biologique. J'indique des cas probables et esquisse leurs implications pour les stratégies d'élevage et d'élargissement des agents de biocontrôle.

Introduction

It is a familiar empirical observation in biological control literature that introduced populations of biocontrol agents can exhibit differences from source populations relatively soon after they are established. Examples of apparently adaptive phenotypic changes are those in the shelter-seeking behaviour of the St. John's wort beetle *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) in British Columbian populations exposed to extremely low winter temperatures (Peschken 1972), and in the temperature threshold for adult emergence of the Californian population of cinnabar moth *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae) (Myers 1978). In addition, some species remain in low but detectable numbers, or enter an 'eclipse phase' during which they are undetectable for a number of generations after release, and then expand rapidly. This has been interpreted by some authors (e.g. DeBach 1965; Wilson 1965) as further evidence for 'post-colonization adaptation'.

An awareness of this need for organisms to adapt to new environments, together with observations from the population genetics literature on the distribution of kinds and amounts of genetic variation, led in the 1960s to a variety of ideas on strategies to maximize genetic variation, and hence subsequent adaptation, in the released population. These ideas are reviewed by Myers and Sabath (1981) in the light of available evidence on electrophoretic variation, phenotypic plasticity, and the genetic variance for quantitative characters. They concluded that there was little evidence that genetic variance was eroded by being passed through the sizes of bottlenecks usually involved in biocontrol introduction, although directional selection imposed during laboratory rearing could have a deleterious effect on subsequent establishment in the field. Recent developments in two areas of evolutionary genetics bear directly on these questions: studies aimed at the management of genetic variation in rare and endangered species, and investigations of the genetic phenomena associated with adaptation following very small bottlenecks.

The first of these areas has led to conclusions generally supporting those of Myers and Sabath (1981), in particular that single bottlenecks have very little effect on either heterozygosity or genetic variance (Frankel and Soule 1981). Moreover, quantitative guidelines for the minimum genetically effective population size (N_e) required to maintain variation have also been derived: to avoid inbreeding depression and maintain genetic variance in the short-term $N_e > 50$, and to maintain long-term adaptability $N_e > 100\text{–}500$ (Franklin 1980; Lande 1976 and pers. comm.). These values are probably in accord with most (successful) biocontrol practice (P. Harris, pers. comm.). As well, there is additional evidence that genetic variation is eroded through adaptation to artificial environments and that this presents a problem for attempted release programmes (Frankham *et al.*, *in press*).

On the other hand, special genetic events can accompany introductions based on a small number of founding genomes. Since these events lead to rapid adaptation to new environments and since the necessary conditions appear to have accompanied at least one classically successful biocontrol introduction, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) in Australia (Murray 1982), it seems worth exploring in more detail their relevance to past and future introductions.

The Nature of Founder Effects and Genetic Transilliences

Population bottlenecks occur when a large population is temporarily reduced to a small size or when a geographically separate new population is founded by a small number of individuals. When a population experiences such a bottleneck the frequencies of alleles at polymorphic loci are subjected to random shifts through sampling error. At such a time, rare alleles may be lost, or occasionally fixed, but reductions in heterozygosity and the additive genetic variance for quantitative characters are not great (Nei *et al.* 1975; Franklin 1980). More variability is lost if the population remains small for a number of generations, or if it is subjected to repeated bottlenecks.

These random effects would be of little interest in natural populations but for the fact that they can strongly influence the outcome of subsequent selection. Mayr (1954) pointed out the potential interplay of random and selective forces. He noted in particular that random effects on allele frequencies at one of a number of loci that interact in the determination of a character subject to selection, will be followed by rapid selective readjustments in the frequencies of alleles at the other interacting loci. He termed this the 'founder principle' and used it to account for rapid, phenotypic changes (genetic revolutions) in geographic isolates of tropical birds.

More recently, detailed genetic analysis of the rapid speciation undergone by flies of the genus *Drosophila* (Diptera: Drosophilidae) in the Hawaiian Islands has led to a clarification of these ideas. Speciation in this group appears to have accompanied the founding of new populations by a small number of individuals followed by a rapid expansion of population size in the new environment: the 'founder-flush' cycle (Carson 1968). Carson (1975) noted that the genetic consequences of these cycles are different for different parts of the genome: morphological evolution and speciation have been rapid, but electrophoretic and karyotypic evolution have been much slower in spite of much within-species polymorphism. He suggests that the genome can be regarded as having a 'closed' and an 'open' component. The open component consists of additive genetic variance and most electrophoretic variation, and responds to selection and random influences in accord with general 'bean-bag' theoretical expectations. The closed component, on the other hand, consists of special inter-locus epistatic interactions underlying directionally selected morphological and developmental characters, and is therefore resistant to all but the extremely strong forces for change that accompany a founder-flush cycle. Random shifts are seen as generating novel genetic combinations, particularly homozygotes for rare alleles at these closed-system loci. The subsequent flush is mainly necessary for the population to retain sufficient variability to adapt to this new genetic environment. Since mate-recognition characters are part of the closed system in Hawaiian *Drosophila*, mating isolation is a frequent outcome of these cycles.

This theory has led to attempts to generate and analyse founder-flush speciation in laboratory populations of *Drosophila*. Powell (1978) and Templeton (1979) have been successful. More importantly, not all founder-flush cycles lead to a genetic revolution, and Templeton (1980) has described in detail the conditions under which such rapid genetic readjustments are most likely to occur. These will now be considered in detail. Because of ambiguities surrounding earlier terminology, Templeton (1980) has referred to these phenomena as 'genetic transiliences'.

Conditions Favouring Genetic Transiliences: What Sorts of Organisms, Characters, and Environments?

Both genetic and ecological characteristics are crucial in predisposing an organism to such events. So are the characteristics of the new environment. Table 1 summarizes the factors noted by Templeton (1980) as affecting the chance of a transilience when a population is established by a very small number of founders. These factors influence first, the chances of a bottleneck generating a novel homozygous genotype and second, the chances of maintaining that genotype while restoring linkage equilibrium in the remainder of the genome during the population flush.

Templeton's (1980) discussions concentrate on changes in the epistatic interactions underlying characters involved in sexual recognition, and hence pre-mating isolation. However, such interactions also occur in the genetic control of other characters, and these too should be subject to transiliences, although premating isolation may not be a direct result. Mather (1973) reviews evidence that strongly epistatic genetic architectures characterize responses to strong directional or disruptive selection. These include the natural genetic architectures of such 'fitness' characters as viability and fertility, and of naturally polymorphic complex phenotypes such as sex differences, host races or other phenotypes controlled by complex supergenes. We should therefore expect that transiliences influencing these characters will occur, and that some will lead to incipient post-mating isolation between parent and daughter populations, especially where, for example, viability in a novel biological or physical environment is selected for in the daughter population.

These considerations also point to particular groups of organisms as being more susceptible to transiliences than others. In Lepidoptera, strong epistatic interactions between X-linked and autosomal loci are common (e.g. Grula and Taylor 1979, 1980*a*, *b*) in spite of the small genetic size of the X-chromosome. Pearse and Murray (1982) have pointed out that this is expected to be a general state of affairs given the lack of dosage compensation of X-linked genes in Lepidoptera (Johnson and Turner 1979), the amount of any X-linked gene product serving as a potentially interactive signal to autosomal genes with different optimal levels of expression in males and females. The predominance of these interactions should make Lepidoptera particularly susceptible to transiliences, especially in sex-limited or sex-influenced traits. A similar argument should apply to birds, which also lack dosage compensation of X-linked genes (Baverstock *et al.* 1982).

Table 1. Attributes of the ancestral population, the founding sample, and the introduced population, that affect the probability of a genetic revolution.

	Probability of Genetic Revolution	
Ancestral Population	High	Low
Size	Large	Small
Mating structure	Panmictic	Inbred
Genetic variability	High	Low
Founding Sample		
Size	Small	Large
Source	Single population	Mixed populations
Introduced Population		
Average No. offspring	Large	Small
Reproductive value of founders	High	Low
Capacity to expand rapidly in new environment	High	Low
Initial density	Low	High
Initial population structure	Subdivided	Panmictic
Generations	Overlapping	Discrete
Mating	Assortative	Disassortative
Chromosome number	Large	Small
Total genomic map length	Large	Small
Crossover suppressors	Few, easily lost	Many, not easily lost
[1] Selection on mate recognition system	Directional	Stabilizing
[1] Sexual behaviour	Partially learned	Totally Genetic

[1] Characters leading to pre-mating isolation between introduced and ancestral populations.

Are There Examples of Transiliences in Biocontrol Introductions?

Whilst there is an obvious demographic parallel between a founder-flush cycle and a successful biocontrol introduction, the combination of conditions described in Table 1 as maximizing the chances of a genetic revolution during such a cycle are met with more rarely. Ideally, candidates for biocontrol agents have all the listed ecological attributes centering on the capacity for rapid increase in the new environment. However, current strategies for maintaining existing genetic variability by introducing large representative samples from ancestral populations would work against the possibility of a transilience. As well, it is difficult to assess the probability that transiliences have occurred because we often know very little about the genetics and ecology of the populations from which previous introductions have been derived. In spite of this, there is good circumstantial evidence that they have occurred in some cases, whilst in others they almost certainly have not. Some examples are described below.

Cactoblastis cactorum

Murray (1982) described evidence for genetic differentiation in life-history traits between Australian populations of *C. cactorum*, and suggested that transiliences could have occurred during and subsequent to the moth's introduction to Australia. Although we are ignorant of many features of the moth's population structure and genetics in both Argentina and Australia, the following more detailed comparison with the attributes listed in Table 1 is possible.

Known factors favouring the occurrence of a transilience are: whilst the characteristics of the ancestral *C. cactorum* population are not recorded, on the basis of its biology in Australia it must have had high levels of genetic variability and was probably wide-ranging as an adult; the founding sample was small, although not extremely so (between 14 and 55 females), but came from a single population representing only one of a number of apparent host-races in South America (McFadyen 1984); the species has a high r_m and underwent a spectacular population flush after release; it was adapting to a new species of host cactus, *Opuntia stricta* (Haworth) Haworth (Cactaceae); natural colonization would have resulted in further local founder-flush events in a peripherally subdivided population structure, as would the major oscillations of cactus and moth populations that followed in the early 1930s (Dodd 1940), and that still take place in some isolated populations today (Murray, unpubl. data). Lepidoptera have high chromosome numbers and a genetic architecture favouring epistatic interactions.

Known factors working against transiliences are the non-overlapping generation pattern, the artificial spread of large batches of eggs and larvae, and the lack of crossing over in female Lepidoptera.

Subsequent introductions of *C. cactorum* to other countries for cactus biocontrol were generally carried out with large samples. However, in Hawaii and the West Indies, natural inter-island colonizations have apparently produced further opportunities for rapid genetic change (Murray 1982). Preliminary observations in the Hawaiian Islands reveal that Oahu moths differ from Maui and Hawaii moths in their phenology and their capacity to feed on different forms of *O. megacantha* Salm-Dyck.

Species Known to have Undergone Very Small Bottlenecks During their Establishment

Cochineal insects, *Dactylopius* spp. (Hemiptera: Dactylopiidae), provide some of the most spectacular examples of biocontrol successes. Many of these introductions have involved a very small number of founders (Moran and Zimmermann, pers. comm.). Notable examples are the introduction of *D. opuntiae* (Cockerell) to Mauritius from Ceylon, which was based on a single fertilized female, while *D. austrinus* De Lotto in South Africa is derived from five females.

The successful release of *Hypogeococcus festerianus* (Lizer y Trelles) (Hemiptera: Pseudococcidae) in Australia was based on the progeny of six females. Interestingly, these were maintained during rearing as single-female lines to remove a parasite

(McFadyen, pers. comm.), a procedure shown in Table 1 as contributing to the probability of a genetic transilience.

Comperiella bifasciata How. (Hymenoptera: Encyrtidae) is a parasite of California red scale *Aonidiella aurantii* (Mask.) (Hemiptera: Diaspididae). DeBach (1965) notes that the release stock of over two million individuals was based on only five females. As well, the stock entered an eclipse phase for 5–6 years before spreading rapidly through southern California.

Chrysolina spp.

The chrysomelid beetles *C. hyperici* (Forster) and *C. quadrigemina* have mostly been spread both within and between continental areas as mass introductions (Clausen 1978), and they would therefore seem unlikely candidates for the sort of genetic reorganization being considered. However, two phenomena suggest that they could be of interest. First, an 'eclipse phase' has occurred during several introductions of these species. When *C. hyperici* was introduced to Australia from England, many separate releases were made, with the animals appearing to become extinct each time. After four years of apparent extinction, a single population erupted and was the base for all subsequent introductions both within and outside Australia (Clausen 1978). A long period of low numbers has also characterized *C. quadrigemina*'s establishment in British Columbia, where its recent spread has been accompanied by changes in phenology that adapt it to survival in non-Mediterranean climates (Harris and Maw 1984; Williams *et al.*, pers. comm.).

Second, in *C. quadrigemina* there is an example of epistatic genetic control in a character associated with fitness differences. In this species there is a colour polymorphism, individuals being bronze or some colour in the green-blue-purple range. Genetic analysis of colour differences in Australian populations (Tomasov, unpubl. data) suggest that a single gene is responsible for the bronze *vs.* coloured difference, bronze being homozygous recessive. A second unlinked locus determines whether coloured individuals will be green or blue/purple. This model has also been found to accommodate the unpublished results of Garthside (1934–36), obtained when he was rearing French *C. quadrigemina* for food tests and for release in Australia. Moreover, the colours are known to be associated with fitness differences and their frequencies vary between populations (Peschken 1972; Williams, Myers and Edwards, unpubl. data; Tomasov, unpubl. data). The ecological genetics of this system deserves far more attention, especially with regard to the ways that the interacting loci influence physiology and development in populations with different phenologies.

Species Unlikely to have Undergone a Genetic Transilience

There are few species for which we have the basic biological information necessary to decide this. However, the cinnabar moth, *T. jacobaeae*, has a low level of electrophoretic variability and has a naturally sub-divided population structure (Myers and Sabath 1981). Whilst these attributes are adequate to maintain quantitative genetic variance, they make *T. jacobeae* a less likely candidate for genetic transilience than other moth species.

Implications for Release Strategies

Most of the species described above have done what is theoretically necessary to undergo a genetic transilience and it would be surprising if they had all failed to achieve it. There is a clear need for work aimed at comparing source and derived populations of biocontrol agents. Such work necessarily involves controlled crosses that explore the genetics of complex characters rather than crude electrophoretic or molecular comparisons. They will therefore be difficult, but it is important to know the answers for two major practical reasons, quite apart from the theoretical interest of whether or not we are making new species. First, if different populations of the same initial species now differ substantially from one another, then care needs to be taken in mixing diverse materials in further introductions. As well, supplementary introductions into long-established populations are sometimes considered because of possible declines in effectiveness. These will probably be useless and may in fact do more harm than good by swamping existing local adaptations.

Second, if genetic revolutions in traits with epistatic genetic architectures have been important in the establishment of biocontrol agents, then strategies to maximize the chances of this can be devised.

Two alternative strategies for weed biocontrol releases are suggested by genetic considerations. First, if the aim of the release is to transplant an organism to an environment (climate, host plant) known to resemble that of the source population, then attempts to represent heterozygosity and genetic variance and to avoid inbreeding depression are desirable. This can best be achieved by: (1) mixing individuals from different source locations; (2) maintaining them as a large stock which is prevented from adapting to artificial rearing conditions (e.g. by rearing in field cages near the ultimate release site); and (3) making only a few releases composed of a large number of individuals. This procedure would allow adaptation based on the additive component of genetic variance.

The second strategy, which would maximize a response based on epistatic interactions between loci, would be more appropriate where the new environment is known to differ in some major way from that of the source population. This strategy would involve: (1) taking a small sample from a single source population; (2) expanding it rapidly in the new environment; and (3) either splitting it into many separate lines shortly after release, or establishing many lines from a number of separate small initial samples. This method would lead to extinction of most of these small release populations but the few surviving populations would be expected to be better adapted to the new environment than a population derived under the bulk-breeding programme described in Strategy 1. A similar idea was suggested by Lewontin in the discussion attached to DeBach (1965).

Interestingly, as pointed out earlier, some of the features of the multi-line strategy have occurred naturally in successful biocontrol releases. For example, splitting of the release stock into several single-female lines may occur, as with *H. festerianus*. The 'eclipse phase' may also represent a period in which a number of release populations are reduced to very small size, with only one undergoing an adaptive genetic revolution. If this population then serves as the basis for subsequent natural or artificial spread, as occurred with *C. hyperici*, then Strategy 2 will have been carried out.

Summary and Conclusions

(1) There is a class of rapid genetic change (a 'genetic transilience') that occurs in some populations subjected to a founder-flush cycle.

(2) The conditions accompanying some biocontrol introductions are such that some transiliences should have occurred.

(3) There is evidence from the comparison of derived populations of biocontrol agents that genetic differences have arisen, but more information is required to assess their nature and extent.

(4) Given the right sort of organism, release programmes can be planned to maximize the chance of generating novel adaptations to new environments.

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Chapter Four
Conflict of Interest in Biological Control of Weeds

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Conflicting Interests and Biological Control of Weeds

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Abstract

Conflicting interests may arise when self-perpetuating and self-distributing natural enemies are introduced for the biological control of weedy plants. Conflicting interests are conflicts between the interests of different groups of society over the impact of biological control decisions. The inability to recall or limit the actions of introduced natural enemies may induce one or more of the following types of conflicts: (i) conflict over biocontrol of introduced target plants; (ii) conflict over biocontrol of native target plants; (iii) conflict over biocontrol risk to introduced nontarget plants; and (iv) conflict over biocontrol risk to native nontarget plants. These are reviewed. Two basic issues, uncertain impact and conflicting perspectives, are fundamental to these problems. There are two key decision points in the resolution of biocontrol conflicts, the choice of plants to target for biological control, and decisions regarding the use of specific organisms as biocontrol agents. It is important that these conflicts are addressed because they involve substantive issues, and because many potential biocontrol projects and agents are currently stalled due to unresolved conflicts. Different conflict resolution options, (i) authoritative decision, (ii) mediation, and (iii) litigation, are briefly reviewed.

Lutte Biologique: Les Conflits d'Intérêts et les Risques d'Élimination des Plantes Indigènes non Visées

Les conflits d'intérêts qui surgissent en matière de lutte biologique sont dus aux valeurs antagonistes qui existent dans une société diversifiée. Les conflits les plus complexes et qui sèment le plus de discordes dans le domaine de la lutte biologique concernent les risques de destruction des plantes indigènes non-cibles. Sur ce plan, les facteurs qui entrent en ligne de compte sont: la probabilité d'utilisation des plantes indigènes, l'impact de leur utilisation et le degré relatif de tout impact. Parmi les plantes indigènes non visées étroitement apparentées aux herbes acclimatées contre lesquelles on a entrepris une lutte biologique par l'introduction d'insectes, mentionnons le millepertuis perforé, la croix de Malte et les chardons aux États-Unis. Les conflits liés aux plantes indigènes soulèvent l'importante question du rôle approprié de la lutte biologique. Les techniques biologiques sont-elles préférables pour la lutte contre les plantes nuisibles acclimatées ne possédant aucun proche parent indigène? En dépit des frustrations et de la dissension causées par ces conflits, nous devons reconnaître qu'il est fondamentalement judicieux de s'intéresser à cette question.

Introduction

Biological control, the use of natural enemies to control pests, is a valuable method of weed control. Discussions of the nature, protocol, and successes of biocontrol of weeds may be found in Andres (1977), Andres *et al.* (1976), Batra (1982), Charudattan and Walker (1982), Goeden (1978), Harris (1971, 1979, 1984), Huffaker (1957, 1959, 1964), Julien (1982), Klingman and Coulson (1982), Wilson (1964), and Zwölfer and Harris (1971).

Although there are other modes of biological control (Batra 1982), this discussion will focus on introduction of relatively host-specific foreign phytophagous insects for control of plants perceived as weeds. The ability of such introduced insects to subsequently reproduce and spread spatially and temporally is at once one of the advantages and limitations of this mode of biocontrol. The inability to recall and limit the actions of natural enemies once introduced may induce conflicts between different interests.

Conflicting interests here refer to conflicts between interests of different groups of society over impact of biocontrol decisions. These conflicts occur between interests that might benefit and interests that might be impaired due to biocontrol decisions. In the biological control literature such conflicts have been termed 'conflicting interests' or 'conflicts of interest' (Andres 1981; Andres *et al.* 1976; Delfosse and Cullen 1981; DeLoach 1978, 1981; Huffaker 1957, 1959, 1964). Because biological control is generally unknown to the public, most of the conflicts are not yet in the public arena. Most conflicts referred to in this paper are presently conflicts as perceived by the biocontrol of weeds community. It is important that we address the problem of conflicting interests because it involves substantive issues (*cf.* Rawlins 1984), and because many potential biocontrol projects and insects are presently in a state of limbo due to unresolved conflicts.

	Introduced Plants	Native Plants
Target Plants	Conflict over biocontrol of introduced target plants	Conflict over biocontrol of native target plants
Nontarget Plants	Conflict over biocontrol risk to introduced nontarget plants	Conflict over biocontrol risk to native nontarget plants

Fig. 1. Types of conflicting interests in biological control of weeds.

There are two issues fundamental to the problem of conflicting interests in biocontrol of weeds: uncertain impact and conflicting perspectives. The intent of a biocontrol introduction is to control the target plant without causing harm to nontarget plants. Researchers in biological control try to reduce the uncertainty of impact through, for example, host-specificity testing. But actual impact of a biocontrol organism on the target plant as well as on nontarget plants is, of course, imperfectly predictable. We live in a diverse society with a diversity of perspectives which often conflict. This is normal in a diverse and democratic society. Different individuals and groups have different perspectives on the value of different resources such as native plants and communities, honeybees, livestock, and cultivated plants. If we could perfectly predict the biological impact of a biocontrol project or agent these conflicts would nevertheless occur, because any given level of impact has different meaning to different interest groups. However, we are better able to assess the trade-offs involved with a better knowledge of the impact of biological control.

Types of Conflicting Interests

Conflicting interests in biocontrol of weeds may be readily grouped into four types according to conflict over target or nontarget plants, and indigenous or introduced origin of plants (Fig. 1): (i) conflict over biocontrol of introduced target plants; (ii) conflict over biocontrol of native target plants; (iii) conflict over biocontrol risk to introduced nontarget plants; and (iv) conflict over biocontrol risk to native nontarget plants. Most biocontrol projects contain at least one type of conflict, and many projects contain more than one.

Target and Nontarget Plants

Conflict over biocontrol of target plants is more straightforward than conflict over risk to nontarget plants, since intended impact on specific target plants is more defined than risk of unintended impact on nontarget plants. Previous discussions of conflicting interests have tended to focus on conflicts over biocontrol of target plants. Risk to nontarget species from biological control in general has been noted by Clark *et al.* (1984), Howarth (1983), and Pimentel *et al.* (1984). There has been an evolution in the practice of biocontrol of weeds from a period of no host-specificity testing and reliance on the judgement of the few workers in this field during the earliest days, through a period of host-specificity testing out of concern for safety to nontarget cultivated plants, to the present period where nontarget native plants are included in host-specificity testing.

Host range information, including field host records and host-specificity test data, is a critical element in conflicts over risk to nontarget plants. Host-specificity is a complex question, and discussions of host-specificity in biocontrol of weeds may be found in Dunn (1978*a*), Harris (1984), Harris and Zwölfer (1968), Wapshere (1974, 1983), and Zwölfer and Harris (1971).

The host range of the stenophagous insects typically considered for introduction as biocontrol agents varies from specificity for one host plant species to specificity for several closely related host plant genera. For these stenophagous insects, plant systematics is an excellent predictor of relative risk to nontarget plants. There is some slight risk that biocontrol insects might unexpectedly utilize a nontarget plant that is distantly related to the target plant, but nontarget plants that are closely related to target plants are at greater risk.

Risk to nontarget plants may be reduced by limiting the choice of biocontrol projects to target plants with few or no close relatives in the same region, and by the use of biocontrol insects with a very narrow host range. Such risk reduction would come at the expense of fewer biocontrol projects and fewer potential biocontrol insects per project.

Introduced and Indigenous Plants

Introduced plants involved in biocontrol conflicts are usually of some readily identifiable value to some economic group such as beekeepers, the ornamental plant industry, or growers of crop plants. We generally lack specific information about the value of native plants, and their value generally is not so readily linked to specific economic groups as above. The kinds of value that have been attributed to native plants are: (i) aesthetic (Ehrlich and Ehrlich 1981; Myers 1979); (ii) ecological (Ehrlich and Ehrlich 1981; Raven 1976; Slobodchikoff and Doyen 1977); (iii) economic (Ehrlich and Ehrlich 1981; Frankel 1970; Frankel and Soule 1981; Iltis *et al.* 1979; Jain *et al.* 1977; Myers 1979, 1983; Nault and Findley 1981; Schmidt 1980); (iv) ethical (Attfield 1983; Ehrlich and Ehrlich 1981; Myers 1979); and (v) legal (Federal Register 1980, 1983; McMahan 1980; Myers 1979; Versteeg 1984). Another type of value that might be attributed to native plants is scientific value, the value as study plants and populations to scientists and to scientific knowledge. Introduced plants may also be evaluated according to the above types of value.

Conflict Over Biocontrol of Introduced Target Plants

Conflict over biocontrol of an introduced target plant itself occurs when a naturalized plant is differently perceived as detrimental and beneficial by different groups (Table 1). There are presently no active biocontrol projects against tamarisk (*Tamarix* spp.; Tamaricaceae) and scotch broom (*Cytisus scoparius* [L.] Link; Fabaceae) in the United States, largely because of lack of resolution of conflicts over the biological control of these plants (Table 1; also Table 3). In the case of scotch broom, a formerly active biocontrol project was suspended indefinitely due partly to this type of conflict (Andres 1979). Two conflicts of this type have resulted in public participation in their resolution, and may provide alternative models of conflict resolution in the future.

Echium plantagineum L. (Boraginaceae) is a naturalized herb in Australia where it is known as Paterson's curse by those who consider it detrimental, and salvation Jane by those who consider it beneficial. The livestock industry generally considers it detrimental because of its alleged toxicity to livestock and because it competes with more desirable livestock forage. The beekeeping industry considers it beneficial because its flowers are a good resource for honeybees. Conflict over biocontrol of *E. plantagineum* has resulted in a legal battle that has gone to the High Court of Australia (Delfosse and Cullen 1981).

Table 1. Conflict over biocontrol of introduced target plants — North American examples.

Introduced Target Plants	Biocontrol Conflicts
Centaurea solstitialis L. (Asteraceae), yellow starthistle (Maddox *et al.*, *in press*; Reed and Hughes 1970).	*C. solstitialis* flowers considered important resource for honeybees (Pellett 1920; Vansell, 1931).
Cytisus scoparius (L.) Link (Fabaceae), scotch broom (Andres 1979; Holloway 1964*a*; Mountjoy 1979; Robbins *et al.* 1970).	Weedy as well as less aggressive varieties of *C. scoparius* grown as ornamental shrubs (Bailey 1949; Clark 1979).
Tamarix spp. (Tamaricaceae), tamarisk, salt cedar (Anderson and Ohmart 1976; Hefley 1937; Lindauer 1983; Robinson 1965; Turner 1974; Watts *et al.* 1977).	Weedy *Tamarix* spp. considered good nesting habitat for a native gamebird, the white-winged dove (*Zenaida asiatica* L.; Columbidae).; tamarisk flowers considered an important resource for honeybees; tamarisks grown as woody ornamentals (Andres 1981; Bailey 1949; Clark 1979; Vansell 1931; Watts *et al.* 1977)

Yellow starthistle (*Centaurea solstitialis* L.; Asteraceae) is a Eurasian herb with spiny heads that is naturalized at highest densities in western North America in rangelands, croplands, and wastelands (Maddox *et al.*, *in press*; Reed and Hughes 1970). Livestock ranchers particularly favor biocontrol of yellow starthistle, and in the 1950s they requested that the University of California's Division of Biological Control initiate a biocontrol project against it. Yellow starthistle flowers are a good resource for honeybees in California's lowlands during the dry summer season (Pellett 1920; Vansell 1931). Beekeepers and the then California Department of Agriculture, with questions about the direct impact on the beekeeping industry and the indirect impact on honeybee-pollinated seed and fruit crops, expressed concern about the biological control of this plant. As a public institution, the University of California was reluctant to carry out a biocontrol program against this plant until the conflict was resolved. In 1959 the California Chamber of Commerce convened its Subcommittee on Weeds to examine this conflict. Participating in this meeting were representatives from the beekeeping industry, cattle industry, sheep industry, County Agricultural Commissioners' Association, California Department of Agriculture, and the Division of Biological Control and the Department of Agronomy from the Berkeley and Davis campuses of the University of California. The net result of this meeting was a consensus agreement that the beneficial aspect of yellow starthistle was outweighed by the losses due to this plant to other segments of the California economy. The members of this meeting unanimously agreed to recommend biological control of yellow starthistle and investigation of plants useful to both the livestock and beekeeping industries in order to replace controlled weeds (California State Chamber of Commerce, 15 Jan. 1959, unpublished minutes of yellow starthistle conference).

Conflict Over Biocontrol of Native Target Plants

Conflict over biocontrol of a native target plant itself occurs when a native plant is differently perceived as detrimental and weedy by one group, but beneficial (at least in some, perhaps more moderate densities) by a different group (Table 2). This conflict is most acute with regard to the possible use of foreign organisms as biocontrol agents. The use of foreign organisms to control native plants that are perceived as weeds, at least at present densities, has been proposed for native plants that are important human allergenic plants (Harris and Piper 1970; Maw 1984) and for native plants that are considered undesirable rangeland weeds because they are unpalatable or toxic to livestock, compete with more desirable livestock forage, or impede the movement of ranchers or livestock (DeLoach 1978, 1981).

The general use of foreign organisms to control native plants would mark a departure from previous biocontrol practices. Such projects would usually also contain conflicts over biocontrol risk to nontarget native plants since most native plants have native close relatives in the same region. Any foreign stenophagous insects introduced to control indigenous plants are less likely to be host-specific to the native target plant since they would occur naturally on different foreign host plants (DeLoach 1981). It might be argued that the intent of use of foreign organisms to control native rangeland weeds is to merely suppress native plants that have expanded their density or distribution because of the disturbance of livestock management practices (DeLoach 1981) back to pre-disturbance levels. But biocontrol of weeds with introduced self-perpetuating organisms is not that finely predictable. The use of foreign seed-feeding insects only (J. DeLoach, USDA, Temple, Texas, pers. comm.), however, might well have the effect of reducing further spread of these plants without greatly reducing their populations, although sufficient host-specificity may be problematical. DeLoach (1978, 1981) has previously reviewed this type of conflict, and Pemberton (1985*b*) also addresses this topic.

Augmentative biological control with indigenous natural enemies (Batra 1982; Frick and Chandler 1978; Templeton 1982) combined with altered rangeland management practices might be an alternative to use of foreign organisms to control native weeds. Use of indigenous pathogens to control indigenous plants perceived as weeds has been considered at least to the stage of apparently successful field experiments for: oaks (*Quercus* spp.; Fagaceae) (French and Schroeder 1969); winged water primrose (*Ludwigia decurrens* Walter; Onagraceae) (Boyette *et al.* 1979); silverleaf nightshade (*Solanum elaeagnifolium* Cav.; Solanaceae) (Orr 1981; Orr *et al.* 1975; Robinson *et al.* 1978); persimmon (*Diospyros virginiana* L.; Ebenaceae) (Wilson 1965, 1969); and jointvetch (*Aeschynomene* sp.; Fabaceae) (Boyette *et al.* 1979; Templeton *et al.* 1978). Augmentation of native insects for biocontrol of weeds is not usually given serious consideration because of the usual presence of native entomophagous natural enemies, particularly parasitoids (but see Frick and Garcia 1975).

The only known intentional introduction of foreign organisms to control native plants occurred in the United States, and this involved the introduction of a foreign population of a native insect onto an island. The so-called Mexican strain of a native cochineal insect (*Dactylopius opuntiae* [Cockerell]; Homoptera: Dactylopiidae) was introduced via Hawaii via Australia from Mexico onto Santa Cruz Island off the coast of southern California, to control native prickly pear cacti and their hybrids (*Opuntia littoralis* [Engelm.] Cockll., *O. oricola* Philb.; Cactaceae). Previous attempts to introduce this cochineal insect from populations on the southern California mainland failed due to lack of establishment of the insect. The introduction of the Mexican strain of *D. opuntiae* has resulted in a reduction of *Opuntia* density by two-thirds to three-fourths of the density before this biocontrol introduction. An important part of this biocontrol success

Table 2. Conflict over biocontrol of native target plants — North American examples.

Native Target Plants	Biocontrol Conflicts
Baccharis glutinosa Pers. (= *B. viminea* DC.) and *B. halimifolia* L. (Asteraceae), baccharis (DeLoach 1978, 1981; Wilken 1972).	*B. glutinosa* considered characteristic component of three U.S. plant communities (Kuchler 1964, 1977); *B. glutinosa* considered locally important floral resource for honeybees and native Hymenoptera (Linsley and Cazier 1972; Vansell 1931); *B. halimifolia* considered characteristic component of one U.S. plant community (Kuchler 1964).
Larrea tridentata (Sesse & Moc.) Coville (Zygophyllaceae), creosotebush (DeLoach 1978, 1981).	*L. tridentata* considered dominant of six U.S. plant communities, and characteristic component of one U.S. plant community (Kuchler 1964); *L. tridentata* a past and potential future source of industrial chemicals (Campos-Lopez and Roman-Alemany 1980; Mabry *et al.* 1977; Timmermann 1977); *L. tridentata* a potential source of biomass energy (Foster and Karpiscak 1983); five spp. of lizards and one sp. of snake restricted to *L. tridentata* flats (Mares and Hulse 1977); many arthropods associated with *L. tridentata*, including 18 spp. of herbivorous insects monophagous on *L. tridentata* (Schultz *et al.* 1977); *L. tridentata* may be important floral resource for native bees (Simpson *et al.* 1977).
Prosopis glandulosa Torr. and *P. velutina* Wooton (Fabaceae), mesquite (DeLoach 1978, 1981; Reed and Hughes 1970).	*P. glandulosa* considered dominant of six U.S. plant communities, and characteristic component of four U.S. plant communities (Kuchler 1964); *P. velutina* considered dominant of one U.S. plant community, and characteristic component of two U.S. plant communities (Kuchler 1964); *Prosopis* spp. considered important nitrogen-fixing plant in generally nitrogen-poor desert soils (Rundel *et al.* 1982; Shearer *et al.* 1983; Virginia *et al.* 1984; Virginia and Jarrell 1983); *Prosopis* spp. considered important resource for wildlife (Martin *et al.* 1951); *Prosopis* spp. considered important floral resource for honeybees (Pellett 1920; Vansell 1931); *P. glandulosa torreyana* considered important shade tree in the U.S. Southwest (Clark 1979); *Prosopis* spp. potential source of biomass energy (Felker *et al.* 1983; Foster and Karpiscak 1983); *Prosopis* spp. locally important source of fuel in Mexico (Campos-Lopez and Roman-Alemany 1980); pods of *Prosopis* spp. potential source of food (Felker and Bandurski 1979; Felker *et al.* 1984).

was the restriction of cattle grazing and the attempted eradication of feral sheep. The arrival on the island of a mainland predator of *D. opuntiae*, the entomophagous moth *Laetilia coccidivora* (Comstock) (Lepidoptera: Pyralidae), has slowed the effect of *D. opuntiae* on *Opuntia* more recently (Goeden 1978*a*; Goeden *et al.* 1967; Goeden and Ricker 1981).

Native plants that are perceived as undesirable weeds, at least at present densities, on U.S. southwestern rangelands include (DeLoach 1978, 1981): acacia (*Acacia farnesiana* [L.] Willd., *A. rigidula* Benth.; Fabaceae); white-brush (*Aloysia gratissima* [Gillies & Hook.] Troncoso [= *A. lycioides* Cham.]; Verbenaceae); ragweed (*Ambrosia* spp.; Asteraceae); sagebrush (*Artemisia* spp.; Asteraceae); locoweed (*Astragalus* spp.; Fabaceae); baccharis (*Baccharis glutinosa* Pers. [= *B. viminea* DC. (Wilken 1972)], *B. halimifolia* L., *B. neglecta* Britton, *B. salicina* Torr. & Gray; Asteraceae); Texan persimmon (*Diospyros texana* Scheele; Ebenaceae); goldenweeds (*Ericameria* spp., *Isocoma* spp.; Asteraceae); tarbush (*Flourensia cernua* DC.; Asteraceae); broomweed (*Gutierrezia microcephala* Gray, *G. sarothrae* [Pursh] Britton & Rusby, *G. sphaerocephala* Gray, *G. texana* Torr. & Gray; Asteraceae); bitterweed (*Hymenoxys odorata* DC., *H. richardsonii* [Hook.] Cockll.; Asteraceae); yaupon (*Ilex vomitoria* Ait.; Aquifoliaceae); juniper (*Juniperus* spp.; Cupressaceae); creosotebush (*Larrea tridentata* [Sesse & Mocino] Coville; Zygophyllaceae); cactus (*Opuntia* spp.); retama (*Parkinsonia aculeata* L.; Fabaceae); mesquite (*Prosopis glandulosa* Torr., *P. velutina* Wooton; Fabaceae); oak (*Quercus havardii* Rydb., *Q. marilandica* Muench., *Q. stellata* Wangenh., *Q. virginiana* Mill.; Fagaceae); groundsel (*Senecio douglasii* DC. [= *S. longilobus* Benth.]; Asteraceae); and nightshade (*Solanum* spp.).

According to DeLoach (1981), the seven best candidates for biological control among weeds of southwestern United States rangelands are the following native taxa: (i) broomweed (*Gutierrezia*); (ii) whitebrush (*A. gratissima*); (iii) tarbush (*F. cernua*); (iv) bitterweed (*Hymenoxys*); (v) baccharis (*Baccharis*); (vi) creosotebush (*L. tridentata*); and (vii) mesquite (*Prosopis*). This ranking was tentative and based upon damage caused by the weeds, beneficial and ecological values of the weeds, and biological control success potential.

Conflict Over Biocontrol Risk to Introduced Non-target Plants

Conflict over biocontrol risk to introduced nontarget plants occurs when one group favors the biocontrol of a target plant, while a different group opposes it due to perceived risk to nontarget introduced plants which are valued by this group (Table 3). This usually occurs when an economic plant that is used for food, ornament, or some other human use is closely related to a target plant. In practice, when field host records or host-specificity test data indicate host utilization of a major economic plant, the potential biocontrol insect is dropped from further consideration for biological control. The situation is more equivocal, however, when host range information indicates host utilization of minor economic plants such as many ornamental plants.

A leaf beetle, *Galeruca rufa* Germar (Coleoptera: Chrysomelidae), is a potential biocontrol insect for field bindweed (*Convolvulus arvensis* L.; Convolvulaceae) in North America. Because this beetle fed and reproduced on several varieties of sweet potato (*Ipomoea batatas* [L.] Lam.; Convolvulaceae) in host-specificity tests, it was dropped from further consideration as a biocontrol agent (Rosenthal *et al.* 1983; Table 3). The leaf beetle *Psylliodes chalcomera* Illiger (Coleoptera: Chrysomelidae) is a potential biocontrol insect for musk thistle (*Carduus nutans* L. complex; Asteraceae) in North America. This insect has never been recorded as a pest of the edible crop globe artichoke

(*Cynara scolymus* L.; Asteraceae) in Europe, where *Carduus* spp., globe artichoke, and the leaf beetle are all native. But because *P. chalcomera* fed and oviposited on globe artichoke in host-specificity testing, this insect has effectively been dropped from consideration as a biocontrol insect (Dunn 1978*a*, *b*; Dunn and Rizza 1977).

The leaf beetle *Chrysolina gypsophilae* Kuster (Coleoptera: Chrysomelidae) is a prospective biocontrol insect for Dalmation toadflax (*Linaria dalmatica* Mill.; Scrophulariaceae) in North America. In host-specificity tests, this beetle fed and reproduced on snapdragon (*Antirrhinum majus* L.; Scrophulariaceae), which is grown as an ornamental herb. There are no field records of this insect on snapdragons in Europe, where both are native (Rizza and Pecora 1984; Table 3). The biocontrol status of *C. gypsophilae* is presently unresolved until this conflict is resolved. The moth *Calophasia lunula* (Hufn.) (Lepidoptera: Noctuidae) was previously introduced into North America for the control of naturalized common toadflax (*Linaria vulgaris* Mill.) despite the fact that larvae fed and developed into adulthood on snapdragon in host-specificity tests (Harris 1963; Harris and Carder 1971).

Table 3. Conflict over biocontrol risk to introduced nontarget plants — North American examples.

Target Plants	Biocontrol Conflicts
Convolvulus arvensis L. (Convolvulaceae), field bindweed (Holm *et al.* 1977; Reed and Hughes 1970; Rosenthal 1983; Rosenthal and Buckingham 1982).	Risk to related nontarget cultivated plants: *Convolvulus* and *Ipomoea* in the tribe Convolvuleae, *sensu lato* (Melchior 1964); sweet potato (*Ipomoea batatas* (L.) Lam.) grown as edible crop plant; *Convolvulus* and *Ipomoea* grown as ornamentals (Bailey 1949; Clark 1979; Rosenthal *et al.* 1983; Rosenthal and Buckingham 1982).
Cytisus monspessulanus L., French broom and *C. scoparius* (L.) Link., scotch broom (Fabaceae) (Andres 1979; Holloway 1964*a*; Mountjoy 1979; Robbins *et al.* 1970).	Risk to related nontarget cultivated plants: unaggressive species of *Cytisus*, *Genista*, and *Laburnum* in the tribe Genisteae grown as woody ornamentals (Bailey 1949; Clark 1979; Polhill and Raven 1981).
Linaria dalmatica (L.) Mill., Dalmatian toadflax and *L. vulgaris* Mill., common toadflax (Scrophulariaceae) (Alex 1962; Harris and Carder 1971; Reed and Hughes 1970; Robocker 1974).	Risk to related nontarget cultivated plants: *Antirrhinum*, *Cymbalaria*, and *Linaria* in the tribe Antirrhineae (Melchior 1964; Munz 1926); snapdragon (*Antirrhinum majus* L.; Scrophulariaceae), an ornamental herb, is the most important closely related cultivated plant (Bailey 1949; Clark 1979; USDC 1982; USDA, SRS 1982); other closely related ornamentals include *Cymbalaria* (*Linaria*) *muralis* P. Gaertn., B. Meyer & Scherb., *L. maroccana* J.D. Hook., and *L. purpurea* (L.). Mill. (Bailey 1949; Clark 1979)

The leaf beetle *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) was introduced into North America for the biological control of naturalized St. John's wort or Klamath weed (*Hypericum perforatum* L.; Clusiaceae), and is the organism chiefly responsible for its successful control in northern California. This beetle was introduced with the knowledge that it fed and reproduced on an ornamental species of St. John's wort (*H. calycinum* L.) in host-specificity tests, although it was thought unlikely to do so in the field (Holloway 1964*b*). Since its introduction, however, *C. quadrigemina* is now found on some field plantings of this ornamental groundcover, and has caused significant damage to it at some sites (Andres 1985).

The lace bug *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae) was introduced at the Serere Research Station in Uganda in 1963 for the control of lantana (*Lantana* *camara* L.; Verbenaceae). Following a massive population buildup of *T. scrupulosa* and the consequent collapse of the lantana population, *T. scrupulosa* was found utilizing nearby experimental plantings of sesame (*Sesamum indicum* L.; Pedaliaceae) in 1965. Adult *T. scrupulosa* fed and oviposited on the sesame, and a small proportion of larvae were able to develop into adulthood on it, though they were not reproductive. This utilization of adjacent sesame plantings occurred again, at least in immediately subsequent seasons. There had been some host testing of *T. scrupulosa* before its release in Uganda, although sesame itself was not tested (Davies and Greathead 1967; Fyfe 1937; Greathead 1971, 1973). Under current host testing protocol, it is likely that sesame would be among the host test plants (Wapshere 1974).

Table 4. Conflict over biocontrol risk to native nontarget plants — North American examples.

Target Plants	Biocontrol Conflicts
Baccharis glutinosa Pers. (= *B. viminea* DC.), *B. halimifolia* L., *B. neglecta* Britton, *B. salicina* Torr. & Gray (Asteraceae), baccharis (DeLoach 1978, 1981; Wilken 1972).	Risk to related nontarget native plants: 20 *Baccharis* spp. native to America north of Mexico (USDA, SCS 1982); two *Baccharis* spp. under U.S. federal review as endangered species (Federal Register 1980, 1983); *B. emoryi* Gray considered characteristic component of one U.S. plant community (Kuchler 1964); *B. pilularis* DC. considered dominant of two U.S. plant communities, and characteristic component of two U.S. plant communities (Kuchler 1977); *B. pilularis* grown as native ornamental shrub (Clark 1979; Schmidt 1980); *B. pilularis* and *B. sergiloides* Gray considered locally important floral resource for honeybees (Vansell 1931); *B. sergiloides* considered characteristic component of two U.S. plant communities (Kuchler 1964, 1977).
Carduus spp., *Cirsium arvense* (L.) Scop., *C. vulgare* (Savi) Ten., *Silybum marianum* (L.) Gaertn. (Asteraceae), various naturalized thistles (Dunn 1976; Frick 1978; Holm *et al.* 1977; Moore 1975; Moore and Frankton 1974; Reed and Hughes 1970; Schroeder 1980).	Risk to related nontarget native plants: these are closely related genera in the subtribe Carduinae (Dittrich 1977); *c.* 130 *Cirsium* spp. native to North America (Moore and Frankton 1974; Ownbey *et al.* 1975); 13 *Cirsium* taxa under U.S. federal review as endangered species (Federal Register 1980, 1983).
Euphorbia esula complex, leafy spurge and *E. cyparissias* L., cypress spurge (Euphorbiaceae) (Best *et al.* 1980; Dunn 1979; Reed and Hughes 1970).	Risk to related nontarget native plants: *c.* 112 *Euphorbia* (incl. *Chamaesyce*) spp. native to America north of Mexico, and 14 *Euphorbia* taxa under U.S. federal review as endangered species; *E. esula* complex and *E. cyparissias* are in the subgenus Esula, as are 21 of the native *Euphorbia* spp. including two spp. under U.S. federal review as endangered species (Federal Register 1980, 1983; USDA, SCS 1982; Pemberton 1985*a*).

Conflict Over Biocontrol Risk to Native Nontarget Plants

Conflict over biocontrol risk to native nontarget plants occurs when one group favors the biocontrol of a target plant, while a different group opposes it due to perceived risk to nontarget native plants which are valued by this group (Table 4). As previously discussed, this risk is expected to be greater for nontarget plants closely related to target plants. This type of conflict is common especially in North America perhaps because many of our introduced weeds originate from Europe, and North America and Europe are floristically similar. This type of conflict will also be common if biological control projects involving the use of foreign biocontrol organisms against native weeds takes place, since native weeds usually have native closely related species present here. This type of conflict is especially difficult because of its prevalence, the indirect nature of the conflict, and because the importance of native plants is more controversial and less quantifiable than the importance of cultivated plants. An important consideration in the assessment of these conflicts is that naturalized weeds may have a negative impact on native plants through interspecific competition and preemption of habitat.

The Wisconsin State Department of Agriculture in 1982 consulted with the Wisconsin Department of Natural Resources (DNR) about further introductions of the weevil *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae) into the State for release against musk thistle. The DNR questioned the risk to the rare native dune thistle (*Cirsium pitcheri* [Torr.] Torr. & Gray; Asteraceae) in Wisconsin from *R. conicus*. These two state agencies reached an agreement not to further release *R. conicus* in Wisconsin until more information could be obtained concerning the question of safety to *C. pitcheri* (J. Doll, Univ. Wisconsin, pers. comm.).

A moth (*Tyta luctuosa* Denis & Schiffermuller) (Lepidoptera: Noctuidae) and a mite (*Aceria* sp.) (Acari: Eriophyiidae) are potential biocontrol agents against naturalized field bindweed in North America. Host-specificity tests have revealed that these arthropods may also utilize native species of *Calystegia* (Convolvulaceae), a genus closely related to *Convolvulus* (Clement *et al.* 1983; Rosenthal *et al.* 1983). The status of these prospective biocontrol agents for field bindweed in North America is currently in limbo pending some resolution of this conflict. *Lema cyanella* (L.) (Coleoptera: Chrysomelidae) is a leaf beetle that is a potential biocontrol insect for Canada thistle (*Cirsium arvense* [L.] Scop.; Asteraceae) in North America. In host-specificity tests, this beetle fed and oviposited on native *Cirsium* species (Peschken 1984; Peschken and Johnson 1979). This insect was nevertheless introduced into Canada in 1983 (P. Harris, unpubl., Status of introductions and main indigenous organisms attacking weeds targeted for biological control: Canada, 1984). A subsequent petition to introduce *L. cyanella* into the United States has been denied by the Working Group on Biological Control of Weeds (WGBCW) (discussed later), at least until more is known about its performance following the Canadian introduction (R. Bovey, USDA, College Station, Texas, pers. comm.).

The likelihood of utilization of nontarget plants and the probable impact of utilization are critical components in the interpretation of host range information prior to an introduction decision.

Utilization

The likelihood of post-release actual field utilization of natural populations of nontarget native plants depends on many factors including: (i) vagility of the insect; (ii) number of nontarget potential host species, based on host range information and taxonomic similarity to the target plant; (iii) abundance of each nontarget plant species; (iv) distribution of the nontarget plants relative to that of the target plant; (v) morphological similarity of nontarget plants to the target plant; (vi) chemical similarity of nontarget plants to the target plant; (vii) phenological similarity of nontarget plants to the target plant; and (viii) habitat similarity, including climate and substrate, of nontarget plants and the target plant.

Allopatry between the target plant and nontarget potential host species of particular concern should markedly reduce the likelihood of utilization of the nontarget potential host species. Yet the presence of other nontarget potential host species that bridge the distributional gap between the target plant and the nontarget potential host species of

Table 5. North American records of adult introduced biocontrol insects reared from natural field populations of native nontarget plants.

Target plant	Biocontrol insect	Native nontarget plant	Place	Reference
Alternanthera philoxeroides (Mart.) Griseb. (Amaranthaceae)	*Vogtia malloi* Pastrana (Pyralidae)	*Philoxerus vermicularis* (L.) R.Br. (Amaranthaceae)	Louisiana	Vogt *et al.* (unpubl. data)
Carduus nutans complex (Asteraceae)	*Rhinocyllus conicus* Froelich (Curculionidae)	*Cirsium undulatum* (Nutt.) Spreng. (Asteraceae)	Montana	Rees (1977, 1978)
		Cirsium flodmanii (Rydb.) Arth.	Saskatchewan	Peschken (1984)
C. nutans complex *C. pycnocephalus* L. *Silybum marianum* (L.) Gaertn. (Asteraceae)	*R. conicus*	At least 10 *Cirsium* spp.	California	C.E. Turner, R.W. Pemberton and S.S. Rosenthal (unpubl. data)
Hypericum perforatum L. (Clusiaceae)	*Agrilus hyperici* (Creutzer) (Buprestidae)	*Hypericum concinnum* Benth.	California	Andres (1985)
H. perforatum	*Chrysolina quadrigemina* (Suffrian) (Chrysomelidae)	*H. concinnum*	California	Andres (1985)
H. perforatum	*Zeuxidiplosis giardi* Kieffer (Cecidomyiidae)	*H. concinnum*	California	Andres (1985)
Tribulus terrestris L. (Zygophyllaceae)	*Microlarinus lareynii* (Jacquelin du Val) (Curculionidae)	*Kallstroemia grandiflora* Torr. (Zygophyllaceae)	Arizona	C.E. Turner (unpubl. data)
T. terrestris	*M. lypriformis* (Wollaston)	Three *Kallstroemia* spp., incl. *K. grandiflora*	Arizona	C.E. Turner (unpubl. data)

concern could subvert this otherwise allopatric protection (Fig. 2). If other factors are equal, the greater the number of native nontarget species closely related to the target plant, the greater will be the possibility of host bridging to nontarget potential host species themselves allopatric with the target species.

Table 5 shows the known North American cases where adult introduced biocontrol insects have developed on natural populations of nontarget native plants. This is 7 of the 33 (21%) of the foreign arthropods deliberately introduced and established for the biocontrol of weeds in America north of Mexico (Julien 1982). In each case the nontarget plants utilized are closely related to the target plants. The amount of utilization in these cases is quite variable, being quite low in the case of the moth *Vogtia malloi* Pastrana (Lepidoptera: Pyralidae) on *Philoxerus vermicularis* [L.] R.Br.; Amaranthaceae) (Vogt *et al.*, unpubl. data) and the weevil *Microlarinus lareynii* (Jacquelin du Val) (Curculionidae) on *Kallstroemia grandiflora* Torr. (Zygophyllaceae) (C.E. Turner, unpubl. data); and ranging from 1 to over 1000 adult *R. conicus* reared/100 heads sampled/population between different native *Cirsium* species in California (C.E. Turner, R.W. Pemberton, and S.S. Rosenthal, unpubl. data). Despite the reduced likelihood of encounter between a stenophagous herbivore and rare potential host plants, three of the native *Cirsium* species utilized by *R. conicus* in California are rare and under U.S. federal review as endangered species. So far the number of adult *R. conicus* reared from these rare native thistles is quite low (C.E. Turner, R.W. Pemberton, and S.S. Rosenthal, unpubl. data).

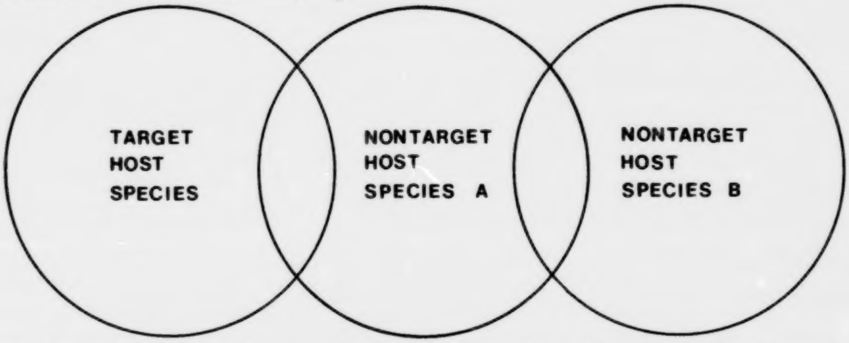

Fig. 2. Host bridge: nontarget host species A may function as a host bridge to nontarget host species B.

It has been hypothesized that the presence of native phytophagous insects on native nontarget potential host plants might competitively exclude introduced biocontrol insects that could otherwise utilize the nontarget plants as hosts (Harris, in Julien 1982; Harris 1984; Peschken 1984). However, other possible outcomes of such interspecific competition between native and introduced insects include coexistence and competitive displacement of the native insects. Moreover, the importance of interspecific competition in phytophagous insects is controversial and has proven difficult to document (Lawton 1984; Strong *et al.* 1984, and additional references therein). There are many cases known where accidentally introduced stenophagous insects utilize indigenous plants as hosts (e.g. Furniss and Carolin 1977), though information about the presence of indigenous insects doing the same type of feeding on these plants is not readily available. The utilization of native plants by introduced biocontrol insects has occurred at least in some cases (Table 5) despite the presence of native insect consumers. The utilization of *K. grandiflora* by the stem-mining weevil *Microlarinus lypriformis* (Wollaston) (Coleoptera: Curculionidae) occurs despite the presence of a native stem-mining longhorned beetle (Cerambycidae) (R.B. Hawkes, unpubl. data; C.E. Turner, unpubl. data.); and the utilization of heads of native *Cirsium* species in California by the weevil *R. conicus* occurs despite the presence of native thistlehead insects (C.E. Turner, R.W. Pemberton, and S.S. Rosenthal, unpubl. data.).

Impact of Utilization

As Andres (1981) has noted, utilization and impact of utilization are different matters. Utilization of nontarget native plants will not necessarily result in significant negative impact on utilized populations or species. The density of a utilized plant population may decline in response to herbivory through outright killing of individual plants or by sublethal feeding damage that reduces plant reproductive output (seeds or clonal units). Although an introduced biocontrol insect may be able to complete development on a nontarget plant species in the field, insect survival rate may be greatly reduced on it compared to survival rate on the target plant species. Rees (1977, 1978) has shown this to be the case with *R. conicus* on *Cirsium undulatum* (Nutt.) Spreng. in Montana, and Vogt *et al.* (unpubl. data) have shown this to be the case also with *V. malloi* on *P. vermicularis* in Louisiana. On the other hand, *R. conicus* on some nontarget native *Cirsium* species in California seem to emerge in about the same high numbers as on its target plants (C.E. Turner, R.W. Pemberton, and S.S. Rosenthal, unpubl. data).

An introduced stenophagous insect may affect a utilized native plant population no more than native herbivores would have in the absence of the introduced insect. In this case, the chief impact of the introduced insect may be on any displaced native insect herbivores and any other species dependent on them (such as insect parasitoids), or the introduced insect may only eliminate individuals from the nontarget plant population that would otherwise have succumbed to other mortality factors acting on the population, such as inter-plant competition. Plants, as primary producers of biotic communities, have had long evolutionary experience with herbivory and generally exhibit apparent defenses and compensatory responses to herbivory (see recent reviews in Crawley 1983; Denno and McClure 1983; Edwards and Wratten 1980; Futuyma 1983; Harper 1977; and Price *et al.* 1980). Different plant species are variable in this regard, and indigenous species will not have had any specific evolutionary experience with an introduced herbivore. Stenophagous herbivores may, of course, have a negative impact on plant populations; the very practice and success of biological control of weeds attests to this.

Theory

Fig. 3 shows some factors that may affect the interaction between populations of a host plant species and populations of a stenophagous phytophagous insect species. There are three theoretical grounds for thinking that introduced stenophagous insects could have a significant negative impact on populations of native nontarget plants that they utilize as hosts. Populations of a monophagous insect and its one host plant species may interact in a reciprocal density-dependent fashion (Andres 1981; Harris 1984; Huffaker and Messenger 1964) such that a monophagous insect would not be expected to drive its single host plant species to extinction (Harper 1977, 1981). No introduced biocontrol insect has extirpated its target weed host in its area of naturalization, although this may have been approached in some of the Hawaiian Islands by two *Microlarinus* spp. introduced to control two naturalized *Tribulus* spp. (Julien 1982). Note that this involved two host plant species for each insect species, and occurred in an insular setting. The presence of an additional host plant species in the same area could change the nature of the host–herbivore interaction, effectively subverting potential reciprocal density-dependence between a stenophagous insect and any one host plant species. A nontarget native plant species that is utilized as a host by an introduced biocontrol insect is more likely to be significantly affected if the target host species or additional nontarget host species are also present in the same area. The potential for this type of situation is obviously heightened for target weeds with many native close relatives combined with biocontrol agents with relatively broad host ranges.

A second consideration is the combined stress of plant interspecific competition and herbivory on a host plant population. Native plants growing in native habitats are typically exposed to interspecific competitive stress from associated plants. The combined stresses of plant interspecific competition and herbivory have a greater impact on plant populations than that of herbivory alone (Bennett 1970; Chater 1931; Goeden *et al.* 1967; Groves and Williams 1975; Harris 1981, 1984; Simmonds 1933; Whittaker 1979). This synergistic relationship also suggests that altered management practices to increase the level of interspecific plant competition upon target weeds should be an integral part of biological control programs, though this is not generally the case currently. In addition to affecting the degree of success of a biocontrol program against a target weed, management practices may also have another effect. Without improved management practices the target weed, if successfully controlled by biological control, may merely be replaced by yet another undesirable weed.

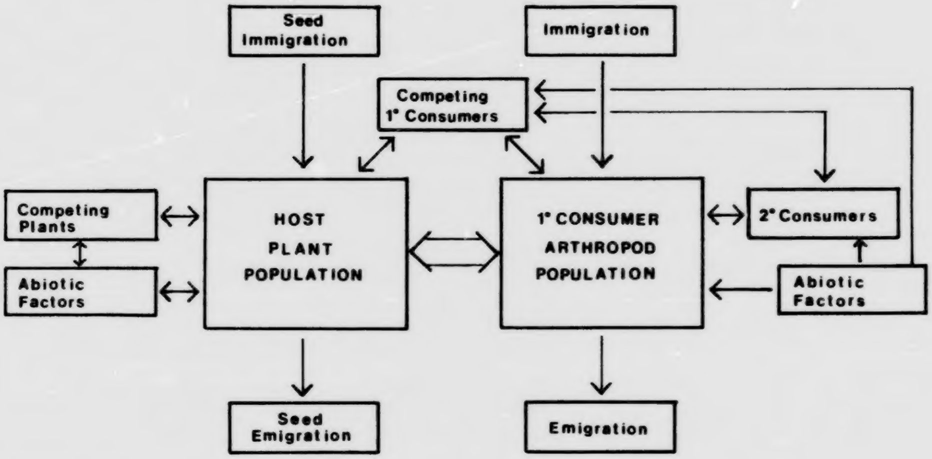

Fig. 3. Plant–consumer interactions.

The third consideration is the regulatory effect that entomophagous natural enemies have on herbivore populations. Natural enemies — predators, parasitoids, and diseases — have an important regulatory influence on populations of herbivores (Edmunds 1973; Goeden and Louda 1976; Huffaker and Messenger 1964; Huffaker *et al.* 1976; Lawton and McNeill 1979; McClure 1977; Myers and Harris 1980; Price *et al.* 1980; Ripper 1956; Simmonds 1933). Indeed, biological control of insect pests is based on this relationship. But it is the intent of workers in biological weed control to attempt to introduce foreign biocontrol insects without their entomophagous natural enemies to increase the probability of successfully controlling the target weed. In contrast to native insects on native plants, introduced biocontrol insects that utilize nontarget plants will usually lack their natural enemies by design. This increases the potential for significant negative impact should host utilization of nontarget plants occur.

Empirical Studies

Studies of the impact of introduced stenophagous herbivores on native plants are most applicable to an empirical assessment of the impact of introduced biocontrol insects on nontarget native plants. Such studies are generally lacking, although they would be significantly informative. There are two types of opportunities for these studies: intentionally introduced biocontrol insects that utilize nontarget native plants (e.g. Table 5), and accidentally introduced stenophagous insects that utilize native plants. The most useful information from such studies are impact of the introduced insect on populations of the native host plant, whether this impact exceeds that from native sources of mortality acting on the host plant, and impact on populations of other native species that interact with the host plant. Also useful would be information about known host range of such introduced insects, and information about factors that might affect likelihood of host utilization and impact of host utilization, as previously discussed. Impact studies are under way at the Albany USDA laboratory on the *Microlarinus* — *Kallstroemia*, *Hypericum* insects — native *Hypericum*, and *Rhinocyllus* — native *Cirsium* systems. The following is a summary of the most severe cases of negative impact of accidentally introduced relatively host-specialized phytophages on North American native plants.

Two introduced fungi have had well-known and devastating effects on two formerly prominant native trees. *Endothia parasitica* (Murr.) A. & A. (Sphaeriales) is the pathogen responsible for chestnut blight of American chestnut, *Castanea dentata* (Marshall) Borkh. (Fagaceae). *Ceratocystis ulmi* (Buism.) C. Moreau (Microaseales) is the pathogen responsible for so-called Dutch elm disease of American elm, *Ulmus americana* L. (Ulmaceae). The smaller European elm bark beetle (*Scolytus multistriatus* [Marsham.]; Coleoptera: Scolytidae) is an introduced insect that has been an important vector in the transmission of Dutch elm disease between trees (Elton 1958; Pirone 1978).

Fraser fir (*Abies fraseri* [Pursh] Poir.; Pinaceae) is a native coniferous tree of limited distribution (Little 1971) on mountaintops in the southern Appalachian Mountains, which may be considered ecological or habitat 'islands' (MacArthur and Wilson 1967; Stebbins 1980). The balsam wooly aphid (*Adelges picea* [Ratz.]; Homoptera: Adelgidae), accidentally introduced from Europe, is regarded as a severe threat to fraser fir (Amman and Speers 1965; Bratton 1982); and the death of stands of fraser fir due to this insect may lead to community-wide changes (Bratton 1982). Balsam wooly aphid also attacks other native species of fir that are more widely distributed (Baker 1972; Furniss and Carolin 1977). The balsam wooly aphid has been the target of an unsuccessful biological control program in North America (Clausen 1978; Schooley *et al.* 1984).

The so-called bermuda cedar scales (*Carulaspis minima* [Targioni-Tozzetti] and *Lepidosaphes newsteadi* [Sulc]; Homoptera: Diaspididae) are two armored scale insects accidentally introduced into Bermuda in the early 1940s. They have virtually extirpated a native tree there, the bermuda cedar (*Juniperus bermudiana* L.; Cupressaceae). The bermuda cedar scales have been the target of a biological control program because of the important scenic value the bermuda cedar had for the tourist industry (Bennett and Hughes 1959; Groves 1955; Rosen and DeBach 1978).

These two known cases where North American native plant species have been threatened by accidentally introduced stenophagous insects involve plants occurring on an actual island and on habitat islands. Many rare plant species occur on unusual habitat islands (Stebbins 1980), such as serpentine substrates, shale barrens, and vernal pools.

Conflict Resolution

There are two key decision points with regard to conflicts in the course of any biocontrol project: the choice of target plants for biological control, and decisions regarding use of specific organisms as biocontrol agents.

In the United States, the WGBCW was established under the joint weed committees of the U.S. Department of Agriculture (USDA) and the U.S. Department of Interior to advise on conflicts over target plants, and to advise on the selection of test plants for host-specificity testing. The WGBCW later expanded its role to advise on decisions about the introduction of foreign biocontrol organisms for study in domestic quarantine facilities and for release into the environment. The WGBCW serves as principal advisor to biocontrol of weeds researchers and to the Plant Protection and Quarantine programs of the USDA Animal and Plant Health Inspection Service (APHIS), which has final legal authority for issuance of federal permits for introduction of foreign phytophagous organisms (Klingman and Coulson 1982). In practice, APHIS has always followed the recommendations of the WGBCW with regard to introduction of foreign insects for biocontrol of weeds.

The WGBCW presently serves a valuable advisory role, but there is no evidence that it is able to resolve serious conflicts. Biological control is not alone in this regard, as society is struggling in general over satisfactory means of resolving technological and environmental conflicts (Abrams and Berry 1977; Cormick 1980; Fischhoff *et al.* 1981; Jasanoff and Nelkin 1981; McCarthy 1976; Okrent 1980; Ramo 1981; Ricci and Molton 1981; Starr and Whipple 1980; Stockholm 1980; Susskind and Weinstein 1981; White 1980).

Three major mechanisms for resolving conflicts in biological control of weeds are: (i) authoritative decision; (ii) mediation; and (iii) litigation.

Authoritative decisions are made by authorized bodies of experts or by administrative agencies with jurisdiction in a particular matter. The functioning of the WGBCW is a weak example of this process, since they are authorized only to make recommendations. Critical to decisions reached by this process are authorization to make decisions, membership of the decision-making group, and membership of those allowed informational input into this group. It is possible that some variation on the WGBCW could function more effectively in resolving biocontrol conflicts.

Mediation is a process by which an independent and neutral party (the mediator) helps to facilitate voluntary and essentially cooperative negotiations between conflicting parties (Amy 1983; Abrams and Berry 1977; Cormick 1980; Fanning 1979; McCarthy 1976; Mernitz 1980; Stockholm 1980; Susskind and Weinstein 1981). The resolution of the yellow starthistle conflict in California, discussed previously, appears to be an example of this process. Mediation has a successful recent record of resolving difficult environmental conflicts (Fanning 1979; McCarthy 1976; Stockholm 1980; Susskind and Weinstein 1981) and appears to hold much promise for resolving biocontrol conflicts. Cormic (1980), Stockholm (1980), and Susskind and Weinstein (1981) discuss the interaction of mediation with the legal system and with agency involvement.

Litigation is a process by which a decision is reached through a legal contest between conflicting parties within the judicial system. Litigation over the *Echium* conflict in

Australia (Delfosse and Cullen 1981) is an example of this process. The main criticisms of litigation as a general means of resolving technological and environmental conflicts are that: (i) it is often very costly in time and money; (ii) it is of an adversarial nature which introduces a gaming element into the process; and (iii) decisions often turn on technical points such as procedural issues rather than on the more substantive issues involved (Abrams and Berry 1977; Jasanoff and Nelkin 1981; McCarthy 1976; Stockholm 1980; Susskind and Weinstein 1981). However litigation may be appropriate when conflicting parties are unwilling to negotiate a compromise or when one party wishes to establish a legal precedent (McCarthy 1976; Stockholm 1980).

Any of these three means of resolving conflicts may be appropriate at times. I suggest a step-wise approach, where authoritative decision is the first step. This process could efficiently decide low conflict cases and at least provide a first screening of high conflict cases. If this process is unable to satisfactorily resolve a high conflict case, I suggest that mediation be tried next if the conflicting parties are willing to attempt negotiating a compromise solution.

Any conflict resolution process should consider advantages and disadvantages of biological control in each case, and alternatives to biological control, including the impact of no control. In conflicts over target plants, advantages and disadvantages of the target plant need to be considered. In conflicts over risk to nontarget plants, advantages of biological control of the target plant need to be weighed against disadvantages of risk to nontarget plants. The severity of conflicts varies between projects and particular prospective biocontrol organisms. For each possible biocontrol project or agent, the greater their disadvantages, the greater should be the advantages of successful biological control to justify the project or use of the biocontrol agent.

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Chemical, Biological or Natural Control of Eurasian Watermilfoil: A study in Biopolitics

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Introduction

This is not going to be a discussion of the relative merits or drawbacks of the chemical, 2,4-D ([2,4-dichlorophenoxy] acetic acid), the white amur (*Ctenopharyngodon idella* Val.; Cyprinidae), or naturally occurring insects for the control of Eurasian watermilfoil (*Myriophyllum spicatum* L.; Haloragaceae) in the Okanagan Valley lakes in British Columbia.

It is going to be about the roles played by scientists, administrators and the public in regard to the infestation and to pest control conflict situations in general.

The Conflict

I shall begin with a brief overview about what happened locally.

Eurasian watermilfoil began spreading rapidly through lakes in the Okanagan basin in the early 1970s. The provincial government, through its Ministry of Environment, established the Aquatic Plant Management Program (APMP) to investigate the situation. Two advisory committees to the program, one composed of various federal and provincial government employees and the other of three University of British Columbia professors, were also established to provide technical advice on aquatic plant management.

By 1977, a number of courses of action had been considered by these bodies. At one end of the spectrum was a minimum program, including general acceptance of the infestation and mechanical control to be done when the weed impeded navigation or presented a severe threat to public safety. At the other was a vigorous control program to reduce the extent of the weed and possibly eradicate it through extensive mechanical and herbicide use.

The first was seen as not acceptable by these planners. The APMP's proposals for 1978 reflected the second — 'an effective and large scale program to attempt to eradicate and to achieve control ... research done has confirmed the effectiveness and safety of 2,4-D and indicated the value of a number of mechanical methods'.

Permits to treat with 2,4-D 500 of the 600+ ha infested were requested. A mechanical control program, research into the ecology of the weed, a quarantine program, use of barriers, elaborate monitoring and safety precautions were also planned.

Use of biological control agents, particularly the white amur and some foreign insects the USDA was investigating, were considered but none were thought to be feasible and efforts in this area henceforth consisted of monitoring U.S. research through the literature.

There was an awareness of the declines that had occurred in other areas, but never any serious consideration given to waiting to see if that might happen here.

Meanwhile, back in the Okanagan Valley, there was considerable concern from various segments of the public about the proposed control program. While most people would rather not have had the weed, degree of reaction varied greatly. Some people felt it threatened their livelihood and others thought it wasn't really all that bad. There was concern about the scale and cost of the proposed program and a feeling in some areas that causes rather than just effect should be dealt with. The city of Kelowna had issued a report saying

> 'we feel ... any action should deal with the habitat or the factors affecting it rather than solely with the offending plants. Cosmetology for the benefit of a few citizens becomes an obligation. It establishes a precedent and requires repetition of the action. Cost in the long term would no doubt be excessive.'

Some members of the Okanagan Water Basin Board also opposed use of public monies for cleaning up private beaches. Local medical health personnel accredited the milfoil with eliminating what had been a severe algae problem in a number of areas and urged that efforts be directed towards dealing with the sewage disposal problems that were causing eutrofication of the lake. The U.B.C. Advisory Committee, after visiting the Valley, acknowledged that there was a definite body of opinion that the control methods must not produce more problems than the weeds themselves.

However, most of the debate focussed on whether the biggest problem was the weed or the 2,4-D that the government planned to use against it. The anti-weed lobby, whose main spokesmen were APMP personnel, painted scenarios of tourists avoiding the Valley, of people drowning in shore-to-shore milfoil, and of property values plummeting. The anti-2,4-D people said none of these dire things would come to pass and that the real danger lay with the 2,4-D which they thought was a possible carcinogen, teratogen, and mutagen. A coalition of local environmental groups led the fray against use of the herbicide, but a wide range of other organizations, including most of the local health people and agricultural groups also went on record opposing it.

The chemical control part of the program was not fully implemented that year or in any of the three years that followed. Twelve, not five hundred, ha were actually treated with 2,4-D in 1978, and only a total of 70 ha were treated over the course of the whole program.

Each year the environmental group would launch appeals against the permits issued. They would produce experts and expert testimony about the dangers of 2,4-D to humans and the environment. The government would counter with other experts and evidence that it was safe. The appeal board which operated under the same government auspices as APMP, always accepted the arguments of the APMP and upheld the permits. However, the delays resulting from these appeals often carried past the time when the chemicals could be effectively applied. As well, the issue of uncertainty of safety and disagreement among experts contributed to public opposition to use of the herbicide. More and more municipal bodies rejected use in areas under their jurisdiction.

The APMP undertook an extensive public relations program to sell the effectiveness, necessity and safety of the program: public information meetings, production of a film about Eurasian watermilfoil called 'The Alien Invader', production and dissemination of pamphlets — but the controversy and polarization, if anything, only increased.

In 1982, the government, using financial restraint as the reason, discontinued the use of 2,4-D for the control of milfoil. The previously unacceptable option had come to pass and milfoil had gone from being a nuisance to a threat and back to a nuisance again. Controls consisted mainly of harvesting. There was still a lot of milfoil in the lakes. However, the infestation had peaked at 674 ha in 1978, and was actually declining since that time in some untreated areas.

The APMP was able to carry on research from 1980 to 1983 into the cause of these declines and clearly established that attack by a variety of indigenous insects, followed by pathogen damage was responsible. This research has now been discontinued. It was not seen as a priority in a time of financial restraint.

To summarize, most of the actual control programs against Eurasian watermilfoil in B.C. have been of a mechanical nature. The large-scale 2,4-D program did not occur, and use of exotic biological control agents was never tested in the area. Natural decline, due primarily to insect attack, is occurring, but whether or not this will significantly reduce the infestation of milfoil in B.C. remains to be seen.

What had also occurred was a tremendous investment of time and energy and money by government and local environmentalists in opposing each other as to how milfoil control would be carried out. This is certainly not a unique situation. Public opposition to programs developed to deal with issues ranging from pest control — milfoil, spruce budworm, gypsy moth — to nuclear plants and the disposal of toxic wastes, has become a familiar pattern in this country, and in many other places in the world.

Discussion

While in the pest control area, chemical control programs have drawn the most fire. This may be at least in part because they are what is most often used. I suggest that the increasing frequency with which we find ourselves at odds with the very people we are supposedly trying to assist is not just an anti-chemical basis; remember, opposition to white amur in many places has been as strong as the opposition to the use of 2,4-D was here. There are a number of situations involving use of biological control agents that resulted in conflicts very similar to this one.

I will predict that as the use of biological control agents becomes more common and higher profile, so will conflicts with the public regarding their use. The agendas of symposiums about biological control, as so many of their agricultural and forestry counterparts already do, will increasingly include discussion about how to deal with what we perceive to be a hostile media, how to outwit 'irrational' environmentalists, and how to reach the silent majority who we hope (but are not sure) support what we are doing. All this and more, unless we can learn why this is happening and make some changes.

The conflict that occurred was not due to malicious contentiousness, incompetence, or anything else of that nature on anyone's part. Indeed, if less capable, less honestly motivated people, had been involved on either side of the conflict, I feel it would not have persisted as long or as intensely as it did.

Nor do I feel that the controversy was without some benefit. Safety measures were perhaps more carefully observed, and alternatives more rigorously sought. Many residents of the area became more environmentally aware because of the issue, and continue to be active in other such situations. However, such gains could surely have been less painfully made, and a program more acceptable to a greater number of people developed and carried out.

With the best intentions we invest a lot of time, energy and money developing programs that we feel sure are the best possible — and they may well be — only to see them rejected, stalled or defeated by the very public they were created to serve. Too often excellent overall programs are put into peril because of one small but controversial part.

Similarly, citizens who oppose these programs truly believe in the truth, beauty, and wisdom of what they are doing, and make similar investments, only to often see unsatisfactory ultimate results.

How can this dilemma be resolved? There are many issues, but I would like to address two that I feel are central to such conflicts. One relates to disagreement among scientists, and the other to decision making.

We need a new theory and method of decision making — one which can accommodate the fact that experts can be expected to disagree — indeed judge such disagreement to be a healthy, inescapable feature of decision making, and that the absence of such disagreement indicates inadequate scrutiny of the situation. In this case, and often in other cases, scientists for the government are pitted against scientists for the opposition, in search of an absolute right and wrong. This seems to spring from some simple theory of science; i.e. that data are collected for which there is one interpretation. In fact, of course, every set of data has a number of often conflicting interpretations. This is something we accept easily enough in discussion among ourselves, but have a great deal of difficulty dealing with publicly.

As well as different interpretations of facts, there are problems of saying what constitutes a significant effect and what is an adequate amount of data.

But basic to all of the above, and most important of all, are the different values and value systems at the root of these disagreements. This is seldom discussed, and when such disagreements occur, too often one's opponent is labelled as biased (which has become synonymous with words like 'irrational' and 'unscientific') and dismissed from further serious consideration.

Actually bias is just a mental tendency or preference — a value system — all things that scientists aren't supposed to have!

'Biased' was the word used by environmentalists and scientists alike about each other in the milfoil conflict. They were both right. There were definitely two kinds of biases or value systems operating in opposition to each other. One was that benefits from use of 2,4-D far outweighed any risks involved: the other was that that was not so. There was also disagreement about the magnitude and urgency of the problem.

Both sides had lots of facts to support their beliefs. However, whether the risks outweighed the benefits, or how urgent it was, was a matter of human judgement, and values and beliefs — an area in which scientists are no more qualified to make decisions than the average layperson, and particularly the average layperson who might be directly affected by the results of any such decision.

Hard facts — ppm, LD_{50}, x number of infested ha — are few and only go so far. Human judgement is needed to interpret facts and findings and determine their relevance to each particular situation.

Also, pest control has been considered to be mainly a technical problem. The APMP personnel certainly tried to deal with it that way. They felt that 2,4-D was (if all technical problems could be overcome) a highly effective control. As is so common in these situations, a decision about how to handle the problem technically was reached first and then an attempt was made to incorporate it with social and economic concerns. The latter are areas like judgement about risks in which biologists have no more wisdom and expertise than the average layperson.

Another thing we are aware of but seldom talk about or deal with constructively is how often where you work, when and where you obtained your education, makes it easy to predict what your priorities, values, biases if you will — will be. In situations like this all possible alternatives are usually acknowledged, but this doesn't mean they are equal or even given serious consideration in daily practice. We always have at least a favourite type of solution which receives more of our attention than other alternatives.

In an attempt to have a wide variety of input and presumably avoid some of the pitfalls I'm discussing, the advisory committees mentioned earlier were established. There were a variety of different specialists involved in the B.C. Aquatic Weed Advisory Committee. However, they shared one definite bias — all were government employees, either federal or provincial, and all had to have at least been aware of, if not in agreement with, the sort of solutions and method of handling public pest control situations that political situations seem to demand; i.e. technological fixes — the application of science in a definite way to get quick and hopefully permanent results. Eradication of milfoil, which was still being talked about as late as 1980 in government reports, is such a solution. The three university scientists had worked on government commissions, indeed were selected partly because of this, and would have also shared this prediliction. It is interesting that when disagreement with the proposed program did arise from within the ranks — some medical health officers, fish and wildlife people, Environment Canada — those in charge of the program dismissed their criticisms as irrational, prejudiced and something to be got around rather than considered.

With scientists and environmentalists alike, initial impressions, once formed, tend to structure the way subsequent evidence is interpreted. New evidence is seen as being reliable if it is consistent with our initial beliefs and not if it isn't. In the milfoil controversy, this was certainly the case. Also depending on their predisposition, people saw efforts to reduce the hazard represented by 2,4-D as either responsiveness to public concern or as an indication that the risks were very great indeed, probably more so than was being publicly admitted.

Differing values or biases among scientists and between scientist and the community at large are inevitable. I don't feel there is anything wrong with scientists functioning as advocates of different points of view or for different segments of the population. It is a problem only if it is not handled openly and evenhandedly.

Which takes me to my second point about who makes the decisions in these conflicts. There is a temptation to say the politicians do, but usually it is not that simple. I would suggest they often prescribe the type of solutions they want — permanent, effective, rapid results — but that the details as to how it will be done — indeed what can be done — are left to the researchers and administrators far more often than we might wish to admit or desire. The charges sometimes made about powerful but invisible elites being behind government actions certainly have some basis in fact. Policy making is not decision making but the former often evolves directly into the latter.

There is also a strong tradition that decisions which will affect environmental quality or public interests are best made by supposedly apolitical, rational, unbiased scientists who will ensure these resources will be used responsibly for the benefit of man. This is a tradition that is being challenged more and more frequently. People are more concerned with the quality of life and see humans as part of the biosphere, not as master of it. They are quicker to resent impersonal, expertise-dominated policies. Many feel about scientists the way many scientists feel about a certain kind of auto-mechanic or physician. They agree there is a problem — possibly not what you thought it was — but don't bother to discuss the details of it with you because they know you wouldn't understand. Besides, it doesn't matter if you do, because they have already decided how to take care of everything, and yes, it's going to cost, and just sign here please. Protests are often less against what is being done than how it is done.

Too often, not knowing how to deal with, or simply not wanting to, we try to neutralize or avoid, public involvement. Most participatory mechanisms are reactive. Too often the pattern is to decide, inform and defend. We hold public information meetings to tell people what we are going to do. Often they already know and, feeling that it is a *fait accompli*, don't bother to show up. Or we ask their opinion, reserving all the time the right to make the final decision.

When it became obvious that there was quite a bit of opposition from the public to the use of the herbicide, the scientists decided that this concern was due to a lack of proper information about the situation and the distortion of facts by the media and environmental groups. The cure was seen to be more information to the public and development of a better relationship with the media. While both are valid actions, they overlooked a desire and need for genuine involvement of people in solving their own problems. They also did not see or refused to accept as something they had to deal with, the fact that it was not that many of the local residents didn't understand the problem but rather that they were disagreeing with the government's interpretation of what it was and with how it planned to handle the problem.

When, then, do you involve citizens? I would suggest you do so from the beginning, before any major decisions have been made and before commitment to any particular type of solution, and on an ongoing basis before finalizing any subsequent steps.

Just what role is a scientist to play in this integrated approach? Lowerance's (1984) criteria from his book 'Of Acceptable Risk', provide a good basic guideline. He feels a scientist's role in any situation involving risk is to: (1) collect and organize information so it is accessible and understandable ... simple and jargon-free; (2) put sources of bias and potential conflicts of interest on the record ... to state previous public positions on the issue at hand; (3) identify what components of a decision are scientific facts and which ones are value judgements; (4) reveal degrees of certainty with which various parts of the decision are known ... to present worst as well as best scenarios and to tell people what we don't know as well as what we do know; (5) insist on the inclusion of critical, articulate laypersons who will be affected by the decision to be included as equal partners in the development of policy and decision making. These could be Turner's (1985) conflict resolution groups or van Zon's (1985) grass carp working group.

From whence are these articulate and critical laypersons to come? I would suggest they are already out there. That, in fact, is the cause of the increase in controversy. It is interesting that it is the more well educated and informed with whom we most often find ourselves at odds. There are more and more people who feel they have a right to know and to have a say in actions that affect them.

For those who feel such people are few and far between, I would like to quote Thomas Jefferson:

> 'if we think people are not enlightened enough to exercise their control with wholesome discretion, the remedy is not to take it from them but to inform their discretion.'

In the Netherlands there are courses which teach scientists how to popularize their research findings and for lay people to better understand and appreciate scientific theory and methods. The latter is very important. Some of our problems may be because we have oversold effectiveness and certainty and safety to the public and consequently have a credibility problem. The public must learn to appreciate that a profession's body of knowledge is only the best available truth for that time and that it is impossible to predict all effects of an action. We must avoid the White Knight Syndrome of saving the lakes, forests, or whatever, and the development of false expectations either by omission or commission.

This will not be easy. Scientist and laypersons alike, like certainty. Uncertainty breeds anxiety which leads to denial which leads to overconfidence in data, methods, and current scientific techniques. However, if we are to solve the problems we face in an amicable and effective manner, we really have no choice but to begin to work in these directions.

It is a matter of reordering priorities. The political aspects of our work will continue to be much more difficult than the biological ones until we decide they are as much of a priority, right from the beginning — as the biological ones. Involving the public must become as important as being sure of the taxonomic identification of the pest or control agent in question.

And finally, I recommend that we look past all the obvious, immediate problems and apparent drawbacks of this new ordering of priorities to the positive aspects of being able to share responsibility in difficult situations, to a surer sense of being on the right track, and for greater support for at least some of the things we might want to do.

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Interaction of *Chrysolina quadrigemina* and *Hypericum* spp. in California

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Abstract

Three insects introduced to control *Hypericum perforatum* (St. John's wort) in California, *Chrysolina quadrigemina*, *Agrilus hyperici*, and *Zeuxidiplosis giardi*, are now reproducing on the North American native *H. concinnum*. Although defoliation by *Chrysolina* seemingly reduces the plant size of *H. concinnum*, the beetle's impact has been difficult to separate from effects of the crown- and root-boring *A. hyperici*. *Chrysolina* also reproduces on two other native *Hypericum* spp. in the laboratory but has not been recorded from these plants in nature. None of the native plants studied are recognized as having economic value. The introduced and now widely cultivated ornamental *H. calcyinum* also serves as a host for *Chrysolina* and occasionally has suffered severe defoliation. At the time *Chrysolina* was introduced to North America (1946), the beetle showed no predisposition to feed or develop on this plant outside of experimental studies. Research is continuing to determine the significance of the presence of *Chrysolina* and *Agrilus* on the *Hypericum* spp.

Interaction Entre les Insectes du Millepertuis Perforé et les Espèces de *Hypericum* d'Amérique du Nord

Trois insectes introduits en vue de lutter contre le millepertuis perforé se reproduisent actuellement sur l'espèce indigène d'Amérique du Nord, *Hypericum concinnum*, en Californie. *Chrysolina quadrigemina* se reproduit sur deux autres espèces de *Hypericum* en laboratoire, ce qui n'a pas été constaté sur le terrain. La forme et l'habitat des plantes semblent être à l'origine des observations différentes en laboratoire et sur le terrain. *Agrilus hyperici* infeste *H. concinnum* en plusieurs sites et a entraîné la mort de la plante. Avant l'introduction, les facteurs dont il faut tenir compte au cours de l'évaluation des risques d'effets préjudiciables de l'agent biologique sur les plantes indigènes non visées sont: (1) le degré de sympatrie entre la plante indigène et la plante nuisible; (2) l'abondance de la plante indigène et la diversité de ses habitats; et (3) la relation qui existe entre l'hôte et la plante nuisible. Dans le choix des organismes candidats, il faut tenir compte entre autres des éléments suivants: (1) type de dommage à l'hôte; (2) synchronisation entre l'organisme et la plante indigène; (3) exigences en matière d'habitat; (4) capacité de dispersion; et (5) comportement de l'insecte en quête d'un hôte.

Introduction

In 1945, *Chrysolina hyperici* Forster (Coleoptera: Chrysomelidae) and in 1946 *C. quadrigemina* Suffrian were introduced into California for the biological control of St. John's wort, *Hypericum perforatum* L. (Clusiaceae), *Chrysolina varians* Schall, *Zeuxidiplosis giardi* Kieffer (Diptera: Cecidomyiidae), and *Agrilus hyperici* Cruetzer (Coleoptera: Buprestidae) were released in 1950, but by that time the dramatic increase and spread of *C. quadrigemina* had already resulted in control at many sites (Holloway and Huffaker 1951). Despite occasional upsurges of the weed following wet winters, control has remained excellent, primarily due to *C. quadrigemina*.

About 1975, we began to receive reports that *C. quadrigemina* was showing up on *H. calycinum* L., an introduced ornamental now widely used for landscaping in urban areas and along highways. At first not much attention was assigned to these sightings, but by 1978, records of beetle damage spanned 11 counties in the northern half of California. A number of these reports were from CALTRANS, the agency responsible for building and maintaining California highways, and involved roadside plantings of *H. calycinum* through the central part of the State. Severe defoliation of the plant was observed in some instances. Although the beetle can still be commonly found reproducing on this plant, the reports of damage have lessened (Andres and Seeno, unpubl. records).

Then, in 1976, *C. quadrigemina* was recorded from *H. concinnum* Benth. in Marin County (E.I. Schlinger, Entomology Dept. of Univ. of Calif., Berkeley, pers. comm.). This plant is indigenous to California and is listed as occurring on dry brushy slopes, below 1000 m (3000 ft) in chaparral and yellow pine forests of the Sierra Nevada and North Coast ranges (Munz and Keck 1959).

Robbins *et al.* (1941) list *H. concinnum* as a weed (gold wire) although, in my opinion, it does not have the aggressive characteristics common to most weeds. Gold wire is sympatric with *H. perforatum* over much of the latter's California range. The extent of *Chrysolina* attack on *H. concinnum* is unknown, although we have observed the beetle at sites in Marin, Napa, Mendocino, Butte and El Dorado counties.

The appearance of *Chrysolina* on plants in the genus *Hypericum*, other than *H. perforatum*, comes as no surprise in light of pre-release studies demonstrating its ability to feed and reproduce on several *Hypericum* spp., including *H. calycinum* (Wilson 1943; Smith 1958). Damage to a planting of *H. calycinum* adjacent to one of the early *Chrysolina* release sites in northern California was reported, but following the reduction of the weedy host, the beetle population on *H. calycinum* collapsed and was no longer a problem (Holloway 1964). *H. calycinum* was not extensively planted around the State when *Chrysolina* was first released but, due to its drought-resistant, fire-retardant characteristics, it is now quite common. It is difficult to explain the upsurge of beetle sightings and damage to *H. calycinum* in 1978. It may have been connected with the 1977–78 drought which seemed to bring the plant growth into closer synchrony with beetle feeding and ovipositional activity.

The presence of *Chrysolina* on *H. concinnum* is of some interest because of the public's increased concern over environmental matters and the preservation of native plants. Since arthropods introduced for the biological control of weeds will continue to show up on non-target native plants, I felt that a retrospective look at the *Chrysolina–Hypericum* relationship might enable us to better assess the propensity of future control agents to expand their list of host species.

Limited observations were made on the behaviour of *C. quadrigemina* in relation to *H. perforatum* and related *Hypericum* species and on the impact of the beetle on *H. concinnum*. The following is a narrative summary of the findings to date. The actual studies will be presented elsewhere when completed.

Behavioral and Developmental Studies

Several replicated and non-replicated tests were conducted on: (a) beetle feeding rates and fecundity; (b) larval developmental rates and percent adult emergence; and (c) adult host finding and ovipositional behavior under field and garden conditions.

Fecundity and Feeding

In non-replicated studies *Chrysolina* females laid markedly fewer eggs on *H. calycinum* than on *H. perforatum* or *H. concinnum*. Replicated studies on these and other *Hypericum* spp. are underway.

Rate of Larval Development and Percent Adult Emergence

Chrysolina eggs were collected from field populations of *H. perforatum*, *H. concinnum*, and *H. calycinum*. Thirty newly hatched larvae were placed on plants of *H. perforatum*, *H. calycinum*, *H. concinnum*, *H. formosum* HBK. var. *Scouleri* (Hook) Coult. and *H. anagalloides* Cham. & Schlecht, in the laboratory (the latter three species are all native to California) and checked regularly for weight gain and completion of development. A magnitude of 2 to 3 times more larvae from the *Chrysolina* population ex. *H. calycinum* completed their development and emerged as adults when reared on *H. calycinum* and *H. anagalloides* than the larvae from the beetle populations ex. *H. perforatum* and *H. concinnum* when reared on the same plants. This suggests that the population on *H. calycinum* has changed to some extent from the population on *H. perforatum*. Adult emergence from the larvae reared on *H. formosum H. concinnum*, and *H. perforatum* test plants was essentially the same no matter from which population and host plants the beetles originated. There appeared to be no significant difference between the three populations in the rate of larval development and the weight of the emerging adults on the five species of test plants.

Host Finding and Ovipositional Behavior

H. concinnum, *H. perforatum*, *H. anagalloides* and *H. calycinum* plants were transplanted among a field population of *H. perforatum* plants infested with *Chrysolina* to rate their relative acceptability for oviposition under 'natural' conditions. Only 4 out of 30 plants of the transplanted *H. calycinum* were oviposited on *vs.* 20 to 27 out of 30 plants of each of the other three transplanted test species. One percent of the total eggs oviposited were found on *H. calycinum*.

A similar transplant study was conducted at the Albany laboratory garden, only in this instance it was necessary to field-collect adult beetles from *H. perforatum* and release them throughout the plot. No eggs were oviposited on the 30 *H. calycinum* plants, whereas eggs were present on 11 to 20 of the 30 plants of the other three test plant species. *H. perforatum* appeared to be slightly favored for oviposition based on the number of eggs laid.

Impact Study

Whether *Chrysolina* is impacting on *H. concinnum* is probably of greater importance than the fact that the beetles feed and reproduce on this native. Larval feeding proved quite damaging and reduced plant size in a study comparing sprayed (malathion) *vs.* non-sprayed *H. concinnum* plants. An unanticipated high rate of attack by the naturalized *A. hyperici* prevented us from determining whether *Chrysolina* alone can kill the plants. *Agrilus* larval feeding in the crown and root probably contributes to reduced plant size and either kills the plant outright or otherwise shortens the life span of this otherwise perennial plant. Further studies are underway.

During the impact study it was noted that *Z. giardi*, the gall midge, was also reproducing on *H. concinnum* in El Dorado County, but in low numbers.

Discussion

Despite the fact that *C. quadrigemina* showed a very low preference for *H. calycinum* in the laboratory (e.g. less feeding, oviposition and larval survival than on *H. perforatum*), it is interesting that a population of this beetle has apparently adapted to live on this plant. This is not quite what we might have expected and signals the need for caution when discussing the plant preferences of candidate biological control arthropods and its significance in relation to post-release behavior.

Chrysolina fed, oviposited and reproduced on all the *Hypericum* species tested in the laboratory, yet it has not been reported attacking *H. anagalloides* and *H. formosum* in the field. Both of these native species are present throughout portions of the naturalized range of *H. perforatum* and quite likely have been exposed to the beetles, although both plants are present more in 'wet meadows, springy places and along streams' than *H. perforatum* (Abrams 1951). This difference in habitat may account for the absence of field records and points up the limitations of predicting insect behavior in nature from laboratory and even field experiments. Whether this can be corrected by increasing our pre-release observations on the natural field behavior of candidate biological control agents in their native range is uncertain. Certainly studies of this nature have been lacking more often than not, and would help us evaluate the role of habitat in determining post-release host range and behavior.

Conclusions

H. concinnum is sympatric with the naturalized *H. perforatum* which has often placed it in direct exposure to *C. quadrigemina* attack over the past 30 yrs. Despite severe damage and varying impact depending on prevailing conditions at the observation sites, the plant is still a common element in those Californian communities to which it is native. I attribute the beetle's limited effect to be due to one or more of the following factors: (1) The form of the plant. *Chrysolina* adults and larvae spend most of their time in the shelter provided by the rosette foliage of *H. perforatum*. The limited basal foliage of *H. concinnum* does not afford such shelter; (2) The plant's phenology. The basal foliage which appears on *H. concinnum* in response to fall rains sometimes appears later than the foliage of *H. perforatum*, again making *H. concinnum* less attractive to the beetles. Both of these factors limit the number of beetles on the plant; and (3) The plant's ability to regenerate from its trailing root system. This factor makes it difficult to kill the plant outright. Once the *H. concinnum* 'mother' plants have been damaged by *Chrysolina*, 'daughter' plants appear along the roots, permitting some plant recovery.

Conceivably, the resiliency shown by *H. concinnum* to attack by *Chrysolina* is more the rule than the exception in describing the response of a native plant attacked by naturalized arthropods. More field studies are needed to document whether this is correct. In the meanwhile, we should proceed with new introductions of new weed control candidates in as responsible a manner as possible.

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Conflict of Interest in CIBC Biological Control of Weeds Programs

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Abstract

CIBC undertakes investigations on biological control of weeds under contract with several countries. Where possible conflict of interest is likely to arise, attempts are made to resolve the issue before a project commences, by ensuring that adequate tests are undertaken, and/or by convincing the authorities concerned that the benefits greatly outweigh any potential detriments. Nevertheless, final authority for introduction of exotic agents rests with the importing country and not CIBC.

Conflits d'Intérêts dans le Cadre du Programme de Lutte Biologique Contre les Plantes Nuisibles de l'Institut du Commonwealth pour la Lutte Biologique

L'Institut du Commonwealth pour la lutte biologique entreprend des recherches en matière de lutte biologique contre les plantes nuisibles pour le compte de plusieurs pays. Lorsque des conflits d'intérêts risquent de surgir, l'Institut tente de résoudre les problèmes avant de mettre en ouevre le projet, en effectuant des essais appropriés ou en persuadant les autorités concernées que les avantages dépassent de loin tous les inconvénients prévus. Néanmoins, la décision finale relative à l'introduction d'agents exotiques relève du pays importateur et non pas de l'Institut.

Introduction

Andres (1981) states that conflicts arise when we are faced with choices or differing points of view. Differing points of view may relate to concern that introductions for weed control may irrevokably reduce plant populations to the extent that the target or its relatives cannot be grown as a crop if a use for it is discovered or, in instances where uses are known, circumstances alter so that it would be profitable or otherwise useful to grow the plant, or that they will destroy allied endemic plants. Other differences or points of view may be based on a general ignorance of the principles and practice of biological control. The case where individuals with a vested interest in current control methods oppose biological control reflects a type of conflict of interest which can impede introductions of agents even after all other indications indicate that the proposed introduction is safe, free from risk, and offers a good possibility of an economic solution to a particular weed problem.

Additional to its activities on biological control of weeds, CIBC also works on biological control of invertebrate crop pests. Conflict of interest of another type can arise if an introduced parasitoid or predator is likely to turn its attention to native or introduced weed control agents. In addition to examples of conflict of interest relating to biological control of weeds and invertebrate pests, I will refer to another CIBC endeavour, the introduction of oil palm pollinators from West Africa into Malaysia, as some of the obstacles faced are relevant.

Conflicts of Interest Within Biological Control of Weeds Programs

CIBC, as a contracting agency, undertakes investigations on biological control of weeds when authorized to do so by a country experiencing a weed problem, or by a funding agency acting in the best interests of a country or group of countries, which cannot or will not fund the relatively high costs of exploration and host range testing of natural enemies. In either instance, CIBC cannot undertake introductions and releases of exotic weed control agents without the consent of the appropriate national agency responsible for authorizing such introductions.

CIBC has undertaken exploration and host range testing on two weeds — *Eichhornia crassipes* (Mart.) Solms Laubach (Pontederiaceae) (Bennet and Zwölfer 1969) and *Mikania micrantha* H.B.K. (Compositae) (Cock 1982) — where funding was supplied by the UK Overseas Development Agency (ODA). These weeds have a comparatively wide distribution in several developing countries, but individually, the countries could not support the research required to ensure the safety of candidate control organisms. In both instances, in contrast to projects contracted by the country where control for the target weed was required, host range testing was hampered by the absence of definitive guidelines from the country or countries where control was required until late in the program, at which time additional costs could be incurred to test plants which were not included in the initial tests. Also, it was not possible to approach all authorities in advance to ascertain whether the question of conflict of interest arose.

Water Hyacinth

After undertaking exploration and limited host-specificity testing of several natural enemies of water hyachinth under a program financed by ODA, agreement was reached to do further testing under quarantine at the CIBC Bangalore laboratory prior to release in India. While these tests were in progress, the regulatory authorities in India, when advised that water hyacinth might have potential for a wide range of uses and products, e.g. animal food, biogas, mulch, paper, etc., decreed that testing of the control agents be terminated. Subsequently, investigations on utilization in India, and elsewhere, suggested that there is at least a limited practical use for this plant and despite frequent inquiries and requests from farmers, etc., for a viable control option in areas where water bodies were completely choked by the weed, the authorities continued to ban further biological control work for several years. Gradually, it became accepted in India, that although there was potential for the use of water hyacinth, it is unlikely that utilization would be feasible in many remote areas or that in other areas the level of utilization would keep the plant in check. A workshop was held in Bangalore in 1982 to resolve this impasse. It was agreed that biological control and utilization were not mutually exclusive options (see Bennett 1982); permission to release *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae) and to proceed with further testing of other candidate agents was granted.

When I was invited to visit the Sudan in 1976 to assist in drawing up proposals for a program for biological control of water hyacinth, ODA (which had indicated interest in funding such a program and gave financial support for the visit) stipulated as one of the terms of reference of the visit that I should ascertain from spokesmen from various organizations working on other approaches to the control and utilization in the Sudan, whether there was adequate potential for utilization in the foreseeable future. ODA wished to make it quite clear that it did not wish to fund a biological control operation which might adversely affect the economy or ecology of the Nile. It was the concensus that although utilization might develop, it would be negligible in the foreseeable future and in view of the enormity of the problem and the high costs of controlling water hyacinth either manually or with herbicides, any form of biological control which offered a glimmer of hope should be vigorously pursued (Bennett 1976). On this basis, a program was instituted. *N. eichhorniae*, *N. bruchi* Hustache, and *Sameodes albiguttalis* (Warren) (Lepidoptera: Pyralidae) were introduced and subjected to further testing under quarantine. Before the first releases were made, permits were obtained from the Plant Protection Department and the Regional Ministry of Agriculture, Animal Resources, Forestry and Irrigation. Also the personnel of the Sudanese German Water Hyacinth Control Project agreed to cooperate and share facilities at El Tawila, north of Kosti, where experiments on biogas production and other utilization aspects were in progress. This program has lead to a drastic reduction of the problem (Beshir and Bennett 1985).

In both of these instances, CIBC considered that introductions did not not present any risk, and recommended biological control programs. However, the final decision of whether to make releases or not, rested with the country concerned.

Parthenium hysterophorus *L. (Compositae)*

This Neotropical composit, because of its rapid growth and its allergenic properties, has become an agricultural weed and a medical hazard. When CIBC was commissioned by the Queensland Department of Lands to undertake investigations of natural enemies in Mexico, the impact that these might have on guayule (*Parthenium argentatum* A. Gray), which has potential as a source of latex, had to be considered. Although this plant had been grown experimentally as a source of latex in Australia, it proved to be an uneconomic crop at the time the trials were undertaken. Nevertheless, the possibility that recent increased costs of synthetic rubber might alter the economics of the situation had to be taken into consideration. Batra (1981), pointing to the potential risks of attempting biological control of a weed congeneric with a crop, cited these *Parthenium* spp. as an example where conflict of interest is involved. However, despite floral similarities, there are major differences in vegetative structure: *P. hysterophorus* is an annual with a non-woody stem, whereas *P. argentatum* is a woody perennial shrub with a tough foliage adapted to xerophytic conditions. Hence, whereas phytophages attacking the stems and foliage of *P. hysterophorus* would be less unlikely to attack *P. argentatum*, those attacking flowers and seeds might. As seed and flower feeding organisms were short listed as candidate species, it was evident that if they did attack *P. argentatum*, latex yields would not be seriously affected. If guayule in the future became a major crop in Australia, and if insects introduced for control of *P. hysterophorus* did restrict seed production, it would be possible by judicious use of chemical pesticides to grow ample seed to plant guayule on a large scale.

In India, a different type of conflict of interest was apparent. Although many farmers have suffered severely from allergies and although CIBC outlined repeatedly the possibilities of biological control, adequate funding to permit introductions of control agents was not forthcoming. On the other hand, numerous 'eradication' campaigns organized by local or regional government authorities have been conducted at a much greater cost in terms of man-power and chemicals than the costs of a full-fledged biological control program. It was apparent that there was more political advantage and immediate short-term impact by uprooting the weed than investing in biological control. The view was also expressed that uses would be found for *P. hysterophorus* and therefore the introduction of weed control agents might be detrimental in the long run. However, because of the seriousness of the problem, and after efforts by CIBC to allay fears of adverse effects of introductions (backed by data on host range tests undertaken in Mexico and by the Queensland Department of Lands in Australia), permission to make introductions under quarantine and to make releases, after evaluation of results of supplementary tests, has been granted.

Papaver sommiferum *L. (Papaveraceae) and* Cannabis sativa *L. (Cannabaceae)*

During the early 1970s, CIBC (funded by the United Nations Fund for Drug Abuse Control), investigated the natural enemies of opium poppy, *P. sommiferum*, and marijuana, *C. sativia*, to ascertain whether species might have potential as biocontrol agents of illicit production of these narcotic plants. Although promising agents were found and host-specificity tests conducted (Buckingham *et al.* 1983), no introduction has been made. Proposed introductions could raise another type of conflict of interest. Illicit producers would certainly protest, possibly in violent fashion, if releases were to be made in or near their 'cultivations'!

Conflict of Interest Arising from Biological Control of Arthropod Programs

CIBC also undertakes projects on biological control of arthropod pests. Questions of safety of organisms proposed for introduction are frequently raised. Will they turn their attention to endemic species related to the target pest, or will they adversely affect organisms introduced for biological control of weeds? It can be very difficult or impossible to predict this, and laboratory trials do not always provide satisfactory answers.

Effects of Introduced Parasites and Predators on Introduced Biological Control Agents

Trichogramma spp. (Hymenoptera: Trichogrammatidae) are routinely introduced from continent to continent against sugarcane borers and other lepidopterous pests. They are frequently mass produced in the laboratory on stored-products pests such as *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), *Corcyra cephalonica* (Staint.) (Lepidoptera: Pyralidae), etc., and in the laboratory will attack a much broader range of lepidopterous eggs than indicated by field collections. The action of *Trichogramma minutum* Riley imported for the control of agricultural pests in Hawaii, is cited as the main reason for the failure of *Bactra truculenta* Meyrick (Lepidoptera: Tortricidae) imported to control nut grass (Clausen 1978). (Other groups of parasites will also attack a broader range of hosts in the laboratory, for example, *Lixophaga diatraeae* Townsend [Diptera: Tachinidae], a parasite of *Diatraea saccharalis* [Fabricius] [Lepidoptera: Pyralidae], can be readily bred on the moth *Galleria mellonella* [L.] [Lepidoptera: Pyralidae], the cassia pod borer *Trachylepida fructicassiella* Rag. [Lepidoptera: Pyralidae], etc.)

Responses to the cues which lead most parasitoids to their host in the field are inherent, and for this reason many species which act as suitable laboratory hosts are not at risk from the same organisms in the field. Nevertheless, in Hawaii the gall fly *Procecidochares utilis* Stone (Diptera: Tephritidae), introduced for the control of *Eupatorium adenophorum* Sprengel (Compositae) is attacked by one or more of the parasites introduced for the control of fruit flies.

There are other examples where species introduced for control of an arthropod pest have included in their diets phytophagous species previously introduced for weed control. *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae), introduced into South Africa on several occasions to control various mealybug pests, attacked

Dactylopius spp. (Homoptera: Dactylopiidae) previously introduced for control of the cactus *Opuntia megacantha* Salm-Dyck (Cactaceae). This host may in fact have aided in its successful establishment leading to the control of the citrus mealybug *Planococcus citri* (Risso) (Homoptera: Pseudococcidae) (Greathead 1971). By the application of selective pesticides, Annecke *et al.* (1969) were able to demonstrate that *C. montrouzieri* and other coccinellids reduce the effectiveness of control of cactus exerted by *Dactylopius* spp. In Maritius, although *C. montrouzieri* failed to establish on the target mealybug, *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae), it established on *Dactylopius* and was suspected to be the cause of an increase in abundance of *Opuntia* spp.

Following successful introduction of *Metrogaleruca obscura* DeGeer (Coleoptera: Chrysomelidae) leading to successful control of the weed *Cordia curassavica* (Jacq.) R&S (Boraginaceae) in Mauritius, plans to introduce a reduviid predator for the control of *Heliothis armiger* (Hubner) (Lepidoptera: Noctuidae) were dropped through concern that it might reduce the effectiveness of *M. obsucra* (Greathead 1971).

Protection of Arthropods Considered to be Natural Resources

Some of the butterflies most prized by lepidopterists occur in Papua New Guinea (PNG). To make material available to the rest of the world, butterfly farming has been encouraged; therefore, to protect this natural resource, legislation governing the collection of butterflies and other wildlife has been passed and is strictly enforced (National Research Council 1983). Hence, any proposed biological control project involving a weed allied to the food plants of a protected butterfly would receive very close scrutiny. Although this type of conflict has not arisen, CIBC has been required to undertake tests with exotic parasites selected for the control of sugarcane borers, *Chilo* spp. (Lepidoptera: Pyralidae) to ensure that they would not develop on butterfly caterpillars. On the basis of laboratory tests, the parasite under consideration, *Apanteles flavipes* (Cameron) (Hymenoptera: Braconidae) was readily cleared and releases were approved.

Similarly, the Institute of Virology, Oxford (IVO) had to satisfy the regulatory authorities that there was no risk before undertaking trials with a nuclear polyhedral virus to control cabbage pests in PNG. When IVO wished to undertake tests in collaboration with CIBC in Trinidad, assurance was sought by the Ministry of Agriculture that the virus would not affect non-target organisms. On the basis that experimental use of the virus had been approved in PNG, tests were permitted in Trinidad.

Oil Palm Pollinators

The African oil palm *Elaeis guineensos* Jacq., when introduced from West Africa into south-east Asia, required assisted pollination to ensure fruitset. Although long considered to be wind-pollinated, CIBC studies conclusively proved that the weevils *Elaeidobius* spp. are the main pollinators in West Africa. As these weevils breed in the spent male florescence (as opposed to the closely allied *Prosoestus* which breed in female flowers), the procedures utilized for screening candidate organisms for weed control were followed. When I approached the Malaysia quarantine authorities for a list of plants to be included in screening tests, I was advised that it would be pointless to send a list because importation of the weevils into Malaysia would not be permitted. This viewpoint conflicted with that of oil palm producers who constitute a very powerful lobby in Malaysia. They sponsored a visit to West Africa and the UK, enabling the quarantine authorities to satisfy themselves that the introduction would not have any serious adverse side effects.

PNG had also expressed interest and was prepared to consider introductions of *Elaeidobius* spp. largely on the basis of CIBC tests. This willingness to proceed also assisted in overcoming the reluctance of the Malaysian authorities, particularly when it was pointed out that each year that introductions were delayed could cost the industry several million dollars, and that officials 'obstructing' the introductions might have cause for later regret!

Subsequently, permission was granted and *E. kamerunicus* (Faust) was released in Malaysia in February 1981. Establishment and rapid buildup followed and within a year hand-pollination was discontinued. Oil palm yields increased by 20% as a result of more efficient pollination. Benefits resulting from the savings on hand-pollination and increased yields have been calculated to be some US$115 million/yr (Greathead 1983).

Discussion

Each proposal for biological control of weeds where conflict of interest may arise will have to be considered separately, and the advantages and disadvantages of biological control compared; alternative control procedures and economics must also be taken into account. When conflict of interest rules against classical biological control, consideration should be given to locally-occurring agents. Recent advances in the development of mycoherbicides indicate that there are viable options to chemical herbicides for the control of certain native and introduced weeds.

It is certain that investigators working on classical biological control of invertebrate pests will have to pay increasing attention to the possibility that introduced parasitoids and predators might adversely affect weed control agents. This is particularly so in those countries where one of the conditions to seek introductions of a control agent is the submission of a statement on the possible adverse environmental impact which could result from the proposed introduction. As an example of an unanticipated impact, the introduction of *Pediobius foveolatus* (Crawford) (Hymenoptera: Eulophidae), which seasonally reduces populations of an important agricultural pest (the Mexican bean beetle, *Epilachna varivestis* Mulsant; Coleoptera: Coccinellidae) to virtual extinction in Florida, may have resulted in an increase of certain weeds which serve as alternative hosts for this beetle (R. Sailor, pers. comm.). In this instance, the economic benefits resulting from a reduction of damage to crops far overweigh any detrimental impact caused by resurgence of the weeds. It is of interest to note that this is one instance where the process could be reversed if desired. *P. foveolatus* does not overwinter in the USA, and if annual releases were terminated, *E. varvivestis* would return to former population levels.

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Echium plantagineum: Catalyst for Conflict and Change in Australia

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Abstract

A brief description is given of Australian agricultural research administration and the way this was used to resolve previous conflicts over the desirability of controlling *Chondrilla juncea* and the possible harm to sunflower from agents proposed for control of *Xanthium pungens*. The scale and complexity of the conflict over *Echium plantagineum* is described and the history of attempts to resolve the issue and final decision to proceed summarized. That the issue was not resolved was shown by subsequent court action which succeeded in preventing implementation of the program. Examination of the legal issues involved showed that legislation would be necessary to protect biological control programs in the future. The status of other weeds and the present interim approval system is briefly described, and the *Biological Control Act 1984* is discussed.

Echium plantagineum: Catalyseur de Conflits et de Changements en Australie

Ce rapport expose brièvement les méthodes de gestion des recherches agricoles en Australie et la façon dont elles sont utilisées pour régler les conflits antérieurs au sujet des avantages de la lutte contre *Chondrilla juncea* et des dommages que peuvent causer aux tournesols les agents biologiques proposés pour lutter contre *Xanthium pungens*. Le rapport décrit la portée et la complexité du conflit au sujet de *Echium plantagineum*, puis donne un bref historique des tentatives faites pour le régler et résume les mesures qui ont finalement été prises. Toutes les tentatives ont échoue; la preuve en est la décision de la cour qui a interdit la mise en oeuvre du programme. L'étude des aspects légaux de la question a montré qu'il fallait adopter des lois en vue de protéger à l'avenir les programmes de lutte biologique. Le document présente un aperçu du projet de loi qui comportera une vaste enquête. Les auteurs décrivent brièvement les méthodes actuelles de lutte contre les plantes nuisibles et le processus d'approbation provisoire.

Introduction

The early settler who first planted *Echium plantagineum* L. (Boraginaceae) in Australia, whether it was Mrs. Patterson in about 1880 (Piggin 1977*a*) or another enthusiast, could not have realized the magnitude of the repercussions that action was to produce a century later, not only with respect to agriculture in southeastern Australia, but for the whole legal framework surrounding the international field of biological control. The controversy over *E. plantagineum* was not the first, nor will it be the last, conflict of interest over biological control of a weed in Australia, but it has certainly been the most important. Appropriately, therefore, it forms the main subject of this account, the principal illustration of problems which have been faced, and changes it has catalyzed.

The biological control program for this species was accepted by a system of decision-making that was apparently effective for previous conflicts, but whose inadequacies became apparent with the *E. plantagineum* conflict. This account follows the evolution of changes in biological control in Australia, dealing first with resolution of earlier conflicts and concluding with discussion of the *Biological Control Act 1984* (Commonwealth of Australia 1984*a*), which should resolve future conflicts of interest in biological control in Australia.

Australian Agricultural Administration

A brief introduction to the administration of Australian agriculture and the environment is necessary to understand the complex history of conflict of interest in biological control in Australia.

For agriculture, the ultimate authority is the Australian Agricultural Council (A.A.C.), comprising the Ministers for Agriculture or Primary Industry from each State and chaired by the Federal Minister for Primary Industry. To A.A.C. are submitted the deliberations and recommendations of the Standing Committee on Agriculture (S.C.A.), made up of the State and Northern Territory Directors of Agriculture, representatives of the Federal Departments of Primary Industry, Health, Trade and Finance, and CSIRO (the national research organization). To this top professional body report other subsidiary committees with responsibility for different sectors of agriculture.

One such committee is the Plant Production Committee (P.P.C.), to which in turn report various technical committees, including the Australian Weeds Committee (A.W.C.), comprising representatives of Departments of Agriculture, Primary Industry and/or other groups of each State and the Northern Territory, plus representatives of CSIRO, the Federal Department of Primary Industry, and forestry interests. The A.W.C. is the principal initiator and co-ordinator of national weeds policies and is also a sounding board for CSIRO and for State reserach programs which are of concern to other States. If necessary (with S.C.A. approval), the A.W.C. may institute technical subcommittees or working parties to deal with specific problems or weeds. The subject of one such subcommittee was skeleton weed, *Chondrilla juncea* L. (Compositae). Thus, for some time there has been a mechanism in Australia for discussion of proposed national and regional biological control programs for weeds.

The system of approval for biological control agents for importation and release has been quite separate from that for target weed approval. The Commonwealth Department of Primary Industry (Plant Health and Quarantine Branch) administers plant and animal quarantine aspects of the *Quarantine Act 1908* (Commonwealth of Australia 1908). Under the provisions of this *Act*, each agent is the subject of an application to Plant Quarantine, which co-ordinates its review by a small committee of senior entomologists for an insect importation or plant pathologists for a pathogen importation. Recently a new act has come into force, the *Wildlife Protection* (*Regulation of Exports and Imports*) *Act 1982* (Commonwealth of Australia 1982), administered by the Commonwealth Department of Home Affairs and the Environment. This *Act* prevents international trade in native, particularly endangered, species, but also has control over importation and release of exotic species and has the power to order environmental impact statements. However, for biological control agents, at least for the present, the Department effectively follows the recommendations of Plant Quarantine.

Thus historically, the two areas for potential conflict of interest have been distinct: on one hand the target weed; and on the other, specificity (i.e. safety) of agents.

Previous Conflicts

The Skeleton Weed Conflict

When biological control of *C. juncea* was suggested to the subcommittee charged with co-ordinating research on the weed, it was opposed by one State on the grounds that the weed was no longer a serious problem and was in fact a good source of feed for fattening lambs for sale and for stock in dry seasons. Later, that State accepted that any loss which might be suffered would be small in relation to the gain elsewhere and the program commenced. In fact, later economic analysis demonstrated enormous economic benefits from control in that State also (Marsden *et al.* 1980).

The Noogoora Burr Conflict

A more serious debate arose over the proposed importation of two insect species for biological control of *Xanthium pungens* Wallr. (Noogoora burr; Compositae), an important weed of the extensive sheep grazing land in Australia (Wapshere 1974). In specificity tests, both species fed on *Helianthus annuus* L. (sunflower; Compositae) and Plant Quarantine could not therefore give permission for importation, but referred it to S.C.A., who then adjudicated on the balance of possible risk to a relatively small sunflower industry against the possibility of controlling an economically very important weed. Permission was given for release.

The Blackberry Conflict

Another major, controversial weed species is blackberry, *Rubus fructicosus* L. agg. (Rosaceae). Field and Bruzzese (1985) have reviewed this conflict of interest. The proposition of biological control of blackberry was advertised publicly in newspapers in the State with the strongest conflict, Tasmania, thus ensuring invitation for as much comment as possible. This was the first weed so advertised in Australia. It could have been a test of the workability of the approval procedure for target weeds and for quarantine (and thereafter S.C.A. adjudication on natural enemies), as it was possible that the major potential control agent, the rust fungus *Phragmidium violaceum* (Schultz) Winter (Uredinales), could have attracted opposition. As it was, with a warning of legal challenge to the program by apiarists in Tasmania it would more likely have become an early candidate for scrutiny under the *Biological Control Act 1984*. Unfortunately, this program has recently become an example of another aspect of this debate, that of the necessity for administrative and legislative procedures to be sufficiently quick and efficient to forestall impulsive action by the farming community, when possible control measures are known. Briefly, early in 1984, *P. violaceum*, the subject of considerable recent research (Bruzzese 1982), was found on blackberry in southern Victoria, almost certainly the result of deliberate, illegal introduction. Persons from other States visited these 'nursery areas', following widespread publicity (including a television program) of the introduction, and moved infected material to their own blackberry infestations. As a result of this movement, *P. violaceum* has been confirmed in northern N.S.W. (J. Walker, pers. comm., 1984).

The Nodding Thistle Conflict

Graziers from northern N.S.W., apparently unhappy at the lack of a biological control program for nodding thistle, *Carduus nutans* L. (Compositae), have threatened to illegally import the weevil *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae) from

New Zealand because they thought that the penalties of illegal importation (if caught) were less than the damage caused by nodding thistle. As the penalties for an individual for such illegal importation are now ten years in jail or a fine of $50,000, or both, either these people are unaware of the penalties, or they have quite a nodding thistle problem!

Other Potential Conflicts

There are several more weed species for which potential conflicts are seen, but their significance is as yet unknown. Several involve species recognized as sources of nectar and/or pollen; e.g. various thistles, and onion weed (*Asphodelus fistulosus* L.; Liliaceae). Others (e.g. capeweed, *Arctotheca calendula* [L.] M. Levyns; Compositae) may be used occasionally as forage, others for sand-dune stabilization (e.g. Bitou bush, *Chrysanthemoides monilifera* [L.] Norlindh; Compositae). These issues await resolution almost certainly under the terms of the *Biological Control Act 1984*.

Given the examples of rational settlement of disputes over skeleton weed and Noogoora burr, how was the *E. plantagineum* case different?

Nature and Scale of the *E. plantagineum* Conflict of Interest

As is clear from the brief summary of the conflict over *E. plantagineum* given by Delfosse and Cullen (1981), the issue was essentially whether on balance the species was detrimental or beneficial, rather than perceived danger to non-target species.

The biology of the plant has been comprehensively reviewed (Piggin 1982). It is a large, conspicuous annual, usually germinating in autumn to produce a broad, spreading rosette capable of blanketing the ground surface and thus restricting more desirable pasture species. It produces a showy inflorescence of generally mauve flowers in late spring, before dying off in summer. It contains pyrrolizidine alkaloids (Culvenor 1956), which are poisonous to grazing stock. Its flowers produce large quantities of nectar and pollen.

The most important claims and counterclaims to emerge from the recent, often bitter, debate can be summarized as follows.

Claimed Detrimental Effects

(*a*) Some pyrrolizidine alkaloids are hepatotoxic carcinogens (Culvenor 1983; Petersen and Jago 1984). Horses (Sharrock 1969; Seaman 1978; Peterson 1984) and pigs (Bull *et al.* 1956) are particularly susceptible to those in *E. plantagineum*, and the alkaloids have contributed to considerable mortality in sheep (Bull *et al.* 1956, 1968; St. George-Grambauer and Rac 1962) and cattle, although sometimes only a very low level of poisoning occurs (Culvenor *et al.* 1984). Verifiable veterinary evidence as to the real scale of this loss has been difficult to obtain.

The alkaloids occur in honey made from nectar of *E. plantagineum*, but at very low levels (Culvenor 1981), and possibly in milk from cows which graze the plant (Peterson 1984).

(*b*) The young plant is very competitive, particularly for moisture and light, hindering the establishment and growth of other species, particularly pasture legumes. It can 'completely crowd out recognized pasture plants such as subterranean clover and rye grass' (Piggin 1968). This in turn decreases the availability of such species for grazing and the input of nitrogen to the soil, the latter in turn decreasing productivity of other pasture species and subsequent crops.

(*c*) The plant is not accepted as good feed for stock. It is often refused when in flower, especially by cattle, and in summer 'leaves very little useful dry matter' (Piggin 1968), in contrast to the seed pods left by pasture legumes. Its undesirability as a forage species clearly compounds the problems of (*b*) above.

(*d*) Despite precautions, it occurs as a serious problem in crops, requiring extra herbicide usage and extra cultivations, or producing contamination and decreased value of broad acre cereal crops and small, high-value seed crops destined for certification.

(*e*) The pollen of *E. plantagineum* is a significant contributor to hay fever problems in spring (Katelaris *et al.* 1981, 1982; Burdon and Burdon 1983), and the bristly epidermis of the dry stem has been accused of producing dermatitis in both cattle and human beings.

(*f*) Given that control is desirable, *E. plantagineum* is often difficult and expensive to control by herbicides. The herbicide 2,4-D can be used to control *E. plantagineum*, but the necessary high rate 'severely reduces the growth of any legumes in the pasture', and 'the weed also becomes more resistant to 2,4-D as it grows older' (Piggin 1968).

Claimed Beneficial Effects

(*a*) The flowers are an extremely good source of light, premium grade honey, used extensively for blending with stronger-flavored *Eucalyptus* honeys and also for direct export. Australia is a major honey producer and *E. plantagineum* can account for 10–15% of the national honey crop (Briggs 1985).

(*b*) In addition to its direct value, *E. plantagineum* is also a valuable source of both nectar and pollen for conditioning hives early in the season prior to the main *Eucalyptus* honey flows, which only occur in amounts significant to be an alternative to *Echium* for conditioning purposes in one out of four years (Briggs 1980, 1985).

(*c*) Nectar and pollen of *E. plantagineum* are of major importance to the maintenance of adequate commercial and feral honey bee colonies for the pollination of agricultural crops in general (Briggs 1980, 1985), and in some regions, no reduction at all in *Echium* populations can be tolerated, because 100% of nectar and pollen produced by all plants is utilized by bees.

(*d*) *E. plantagineum* is a productive, nutritious and useful species: particularly in drier regions (300–350 mm p.a. rainfall), where its early growth in autumn, and its persistence in late spring, provides forage when little other feed is available (Davies and Sim 1931; Trumble and Fraser 1932; McAuliffe 1953; Myers and Poole 1963; Pearce 1972; Piggin 1977*b*, 1978*a*, *b*).

(*e*) *E. plantagineum* can be controlled by integrated techniques, especially by spray-grazing (Pearce 1972; Piggin 1979).

(*f*) Aesthetically, it adds to the beauty of rural landscapes in spring when in flower.

Thus it is clear that the areas of disagreement covered a wide range of Australian agriculture: from stock health to cropping practice, grazing value, weed control, honey production, the pollination of Australian crops, human health and aesthetics. This, over a distribution of perhaps 0.8 million km^2 (Fig. 1), covering an enormous range in timing and extent of rainfall (250–1000 mm p.a.), temperature, soil type, farming practice and coexisting nectar flora. The potential financial scale of the conflict was significant, with figures of $3.5 million for the annual value of *E. plantagineum* honey, $7–8 million for the annual value of lost nitrogen input to the soil in one State, and from 'conservatively' $600,000 (BAE 1984) to an 'undoubtedly overstate[d]' $100–400 million (IAC 1984) to $250 million (Briggs 1980) to $350 million (Briggs 1985) for the annual value of incidental pollination of Australian crops by honeybees, all being claimed at various times.

Doubts over the rights of apiarists to make money from a plant declared noxious in many areas and which caused problems to the actual landholder, and the possible environmental and human health hazards of herbicide use, all added bitterness to the discussion. To obtain reliable data covering all claims would have been an enormous task, and often discouraged people from making any attempt at gaining hard evidence or objectively examining the meagre data available. The situation also raises the question of how much it is justified to spend in quantifying a weed problem, in relation to the size of the problem and the cost of control. Thus in this case, judgements were made mostly on the basis of opinion, anecdotal information and casual observation, mixed with politics and supported by limited data.

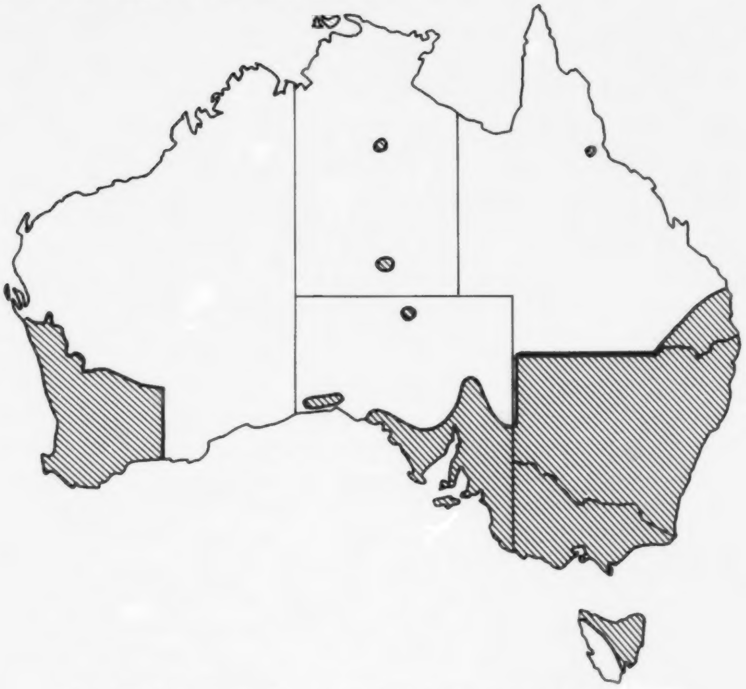

Fig. 1. Main distribution (shaded) of *Echium plantagineum* L. in Australia.

The Decision to Proceed

In 1971, among a small group of priority weeds suggested by members of the A.W.C. as possible targets for biological control were common heliotrope (*Heliotropium europaeum* L.) and *E. plantagineum*, both Boraginaceae. The suitability of *E. plantagineum* as a target weed, in light of the known conflict of interest, was checked with the State where it was most controversial, which gave agreement, and work commenced. Each year the desirability of the program was confirmed by the A.W.C. During 1974–75, following comments about the readjustments which might be necessary in one State if the plant were controlled, all State Directors of Agriculture were asked whether, on balance, control was desirable, particularly with respect to the honey industry. All responded affirmatively, though with varying degrees of enthusiasm. Thus effectively, the decision had the approval of individual members of S.C.A., but formally the discussion had remained at the level of the A.W.C.

However, although information was available at the Department of Agriculture level and the possibility of biological control was raised in an Australian beekeeping journal in 1974 (Clemson 1974), beekeepers claim that they did not become aware of this program until 1978 (Briggs 1980, 1985). The controversy then erupted, with the apiarists' associations lobbying Ministers and the CSIRO to stop the program. Thus in August 1978, the CSIRO Division of Entomology proposed to A.W.C. that S.C.A. should be asked to form a working party to resolve the dispute, and said that they would not release agents unless all States unanimously recommended to proceed (Briggs 1985). The 1978 A.W.C. meeting recommended an expert inquiry to assess the validity of the claims and the new information put forward. The S.C.A. rejected the proposal for an inquiry, recommending initially that the program should not proceed. A.A.C. subsequently did not accept this S.C.A. recommendation, and referred the matter back to S.C.A. for a full report. Six months later, following consideration of a report prepared by one State which included material from a public inquiry held by another State, S.C.A. recommended and A.A.C. accepted, that the program should proceed. In response to further lobbying by the apiarists, the decision was reconsidered six months later but confirmed again. A small element of doubt expressed by one State Minister disappeared with a change in government of that State, and in October 1979 CSIRO was authorized to proceed, with the unanimous agreement of A.A.C.

Legal Action

Meanwhile, the supporters of *E. plantagineum*, who generally refer to the plant as Salvation Jane rather than Paterson's curse, considered the decision of A.A.C. unacceptable, and that they had been overruled by 'big government' without a fair hearing. All avenues of appeal were apparently exhausted and in 1979, the Federal Council of Australian Apiarists' Associations voted to 'support the proposed legal action by the C.A.A. [Commercial Apiarists' Association] of N.S.W. to stop the introduction by CSIRO of biological control agents to control Salvation Jane/Paterson's curse if and when such action becomes necessary.' (Anon. 1979). The *Salvation Jane Preservation and Legal Defence Committee* was formed, with representation from apiarists and graziers from dry areas. After taking legal advice, an application was made to the High Court of Australia by four plaintiffs seeking a permanent injunction, which would in effect prevent biological control of the plant. The immediate result was the granting of an interim injunction on 10 July 1980 and an agreement with CSIRO that it would maintain the *status quo* (no further releases of agents and bagging of plants containing immature stages of one species already released) (Delfosse and Cullen 1981) while the legal situation was examined. In fact the interim injunction remained in force throughout all further exchanges and protracted negotiations.

The Legal Basis for Challenge and Defence

An appreciation of the significance of this court action and its far-reaching effects requires a brief examination of the legal framework within which considerable discussion took place over the next three years.

The onus was initially on one or more of the plaintiffs to establish a cause of action; i.e. a legal basis for complaint. The four plaintiffs (significantly two apiarists and two graziers) made various claims about the value of *E. plantagineum* to them, and therefore the loss they would suffer if it was controlled. While many of these claims were based on anecdotal evidence and could have been difficult to substantiate, there was a strong possibility that some could have been accepted in court. In the case of the two grazier plaintiffs this would have led to the establishment of a cause of action in law, which the CSIRO would then have been obliged to answer. The position of the two apiarists was different, in that whatever their claims, as they were not the owners or leaseholders of the land on which their claims of a significant contribution to their livelihood were based, their chances of success in court were much reduced. They had in fact received legal advice beforehand to this effect and had enlisted the support of graziers.

Given that there was a case to answer (i.e. that an individual with legal standing and substantive claims could legally oppose the program), was there authority to proceed? An A.A.C. resolution in fact carries no legal authorization, nor does the statute governing CSIRO give a legal warrant for biological control. Each State's noxious weeds legislation is a source of positive legal authority to enforce control on an individual's property, but unless it covers all areas where biological control might have an effect (i.e. throughout the distribution of a weed), some areas will remain where control (chemical or biological) has no legal authority.

Noxious weeds legislation in Australia is usually applicable on a regional basis and framed to provide a legal obligation to control a weed where it is recognized that control is desirable and economically feasible. Much of the distribution of *E. plantagineum* is not covered by such legislation (Fig. 2), which is unlikely to change because of these two considerations. Both grazier plaintiffs were in regions where the legislation was not in force. It should be emphasized that what was being sought was a legal authority for positive action (i.e. release of biological control agents) not simply compliance with existing regulatory laws (e.g. those governing quarantine). Compliance with quarantine measures is necessary, but does not give an authority to overrule other objections.

In summary, no mechanism existed in Australia to give a legal warrant for release of a self-dispersing and self-perpetuating biological control agent, which might eventually disadvantage an individual or section of the community, nor are we aware that any such mechanism existed anywhere at that time. In its absence, the rights of the individual in common law are the important factors and the principle of private nuisance allows the individual to take action to prevent the 'unlawful interference with a person's use or enjoyment of land, or some right over, or in connection with it'. The logical defence would be that of public or national benefit, but this has rarely been acceptable to courts, and would not have applied in this case.

Expert legal advice was that CSIRO was likely to lose the case on points of law, quite apart from the difficulty of proving national benefit in such a diffuse area in a court of law. The adversarial approach of the legal process and agricultural and environmental science make very poor bedfellows. Further advice confirmed that the same principle was applicable to biological control programs in general and equally relevant to possible harm to a non-target species, if this was a demonstrated possibility and the non-target species was considered desirable by an individual with a legal basis ('standing') for objection. For example, a sunflower grower could almost certainly have obtained an injunction to prevent importation of insects for *X. pungens*, a rabbit-trapper to prevent importation of myxomatosis virus, and graziers to prevent importation of skeleton weed agents, etc. Thus the most satisfactory solution was appropriate legislation.

Subsequent Developments

The diffusion of this message among the agricultural and political community amidst the atmosphere of a pending court case created some difficulties. Negotiations started two days before the court proceedings produced an agreement not to go to court, but to have the appropriateness of biological control of *E. plantagineum* decided by an independent inquiry. Both sides agreed that a long, expensive and widely publicized court battle would be disadvantageous.

However, continued disagreement over the detailed form and composition of this inquiry, influenced by the plaintiffs' fear of governmental or political influence, resulted in this agreement being rescinded and CSIRO finally agreeing to a perpetual injunction of the court on 22 June 1983, stopping it from proceeding with the program. This injunction also contained the option of seeking a variation in, or complete lifting of the injunction at a later date if authority was given to proceed under future legislation (the groundwork for which was already underway), but required that CSIRO pay the legal fees for the plaintiffs (*c.* $93,000).

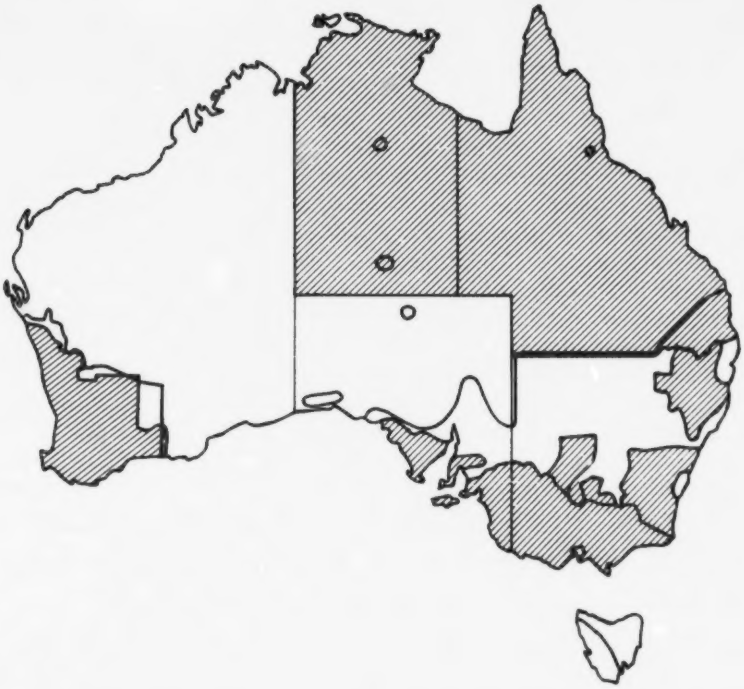

Fig. 2. Main areas of infestation of *Echium plantagineum* L. in Australia (outlined; see Fig. 1), and areas where it is proclaimed noxious (shaded).

After five years of intense debate, including three years of legal sparring, thus ended this very significant phase of the conflict. The old system of 'approval' was left in shreds and a complete rethink was necessary, which eventually resulted in legislation (the *Biological Control Act 1984*). However, an important initial effect was an attempt by S.C.A. in 1978 to defuse future conflicts by proposing that a new system of approval be found. This is currently in force and several target species have been subject to it during the last five years.

Current Approval Procedures

The system as originally introduced in 1979 with regard to approval of candidate weed species for biological control had several aspects in common with relevant aspects of procedures adopted in Canada (Harris, pers. comm., 1983) and in the U.S.A. (Klingman and Coulson 1982). The organization requesting approval prepared a report on the weed, basing it primarily on points previously adopted by Australia in the production of guidelines for the importation of pathogens for the biological control of weeds, and a little later in the series on the biology of Australian weeds, both derived originally from the series on Canadian Weeds (Cavers and Mulligan 1972).

The principal topics on which information was requested were: taxonomy; related species in the Australian region (both cultivated and endemic); original and present distribution; detrimental and beneficial aspects; and control measures. This report was circulated to each member of the A.W.C., who was responsible for ensuring its circulation within his or her own and other Departments of the State. Comments and possible objections were returned to the proposer, who could then modify the report accordingly. The proposal would then be the subject of a recommendation from A.W.C. as a whole; e.g. acceptance, rejection, or that a conflict existed, which may require adjudication at a higher level. In the latter case, it was the A.W.C.'s responsibility to ensure that all available information was assembled so that an informed decision could be made. The final approval was essentially that of S.C.A.

More recently, a slight change was introduced to streamline the system for weeds where there is no conceived opposition to their control. In the first step, the secretary of A.W.C. circulates minimal information on the weed directly to the States, and a full-scale report is prepared only if opposition is signalled. If there is no opposition, the weed can be approved at A.W.C. and P.P.C. level, and S.C.A. informed. If there is opposition, the system is as given above. It should be emphasized that this is only concerned with the potential target weed. Approval for *introduction* of individual biological control agents for weeds is the responsibility of the Plant Health and Quarantine Branch of the Department of Primary Industry. (Approval for *release* of agents for weeds can be obtained, if desired, using the *Biological Control Act* 1984; see below.) To date also, only target species attracting no significant opposition have been through this system. Six such species have recently been approved with five more in line for approval.

Australian Legislation: the *Biological Control Act 1984*

This *Act* preserves the historical distinction between deciding the status of a particular weed species and assessing the possible harm to non-target species by biological control agents. The *Act* is presented in Appendix 1. The date of commencement of the *Act* was 22 November 1984. It applies only to the Australian Capital Territory (including the Jervis Bay Territory) but complementary legislation is expected to be passed by all States and the Northern Territory.

A basic principle is that if the right of an individual to protest an action in common law is to be controlled by legislation, the legislation should ensure that all issues are canvassed, possibly involving a public inquiry, before a decision is taken. However, if a decision to proceed is then made, the program should be able to continue without hindrance and without liability on the part of the individual or the organization involved. Provision for considering compensation is included.

The basic procedures of the *Act* are essentially formalization and broadening of current procedures for approval of a target weed, but applied to all targets for biological control (weeds, arthropods, vertebrates, etc.), followed by a second step to deal with individual agents.

The main procedures set out in the *Act* are summarized below (legal jargon translanted). See Appendix 1 for details.

Definitions and Other Preliminary Material

Several sections of Part I of the *Act* deal with definitions of important terms, biological control, extension of the *Act* to external Territories, references to other laws, etc.

The Commonwealth Biological Control Authority and Target Organisms

Organisms can be declared by the *Biological Control Authority* (B.C.A.) as target organisms for biological control programs. The B.C.A. is established by the *Act* (Part I, section 8), and will be the Commonwealth Minister for Primary Industry from commencement of the *Act* until 1 April 1985. Before 1 April of each subsequent year, the Commonwealth Minister, in consultation with A.A.C., shall designate the Commonwealth Minister, or a Minister of a State who is administering a relevant State law (i.e. complementary biological control legislation) as the B.C.A. for that year.

Action for declaration of target organisms can be commenced in two ways (Part II, section 12): (1) a recommendation to the B.C.A. by A.A.C.; or (2) an application under section 13 of the *Act*.

In the latter case, a signed, written target application can be submitted to the B.C.A. by an individual or a representative of an individual, and must contain particulars such as given above under the current system of approval. An application can be withdrawn any time before it is referred to A.A.C. (section 14). If it is not withdrawn, the B.C.A. must refer the application to A.A.C. for consideration, unless action has been already taken on the organism (or is in train), under this *Act* or a relevant State law (section 15).

If A.A.C. informs the B.C.A. that A.A.C. does not recommend declaration of the organism as a target organism, notice of the outcome is given to the applicant (and to later applicants, if any) by the B.C.A. The B.C.A. must either give the applicant the reasons for rejection (if A.A.C. gave reasons) and the B.C.A. must indicate circumstances under which it feels the organism might be recommended by the A.A.C. for approval (section 16).

A.A.C. can also recommend to the B.C.A. that the organism should be a target organism for biological control (section 17). In this case, the B.C.A. must publish the intent to declare in the Government *Gazette and* in 'appropriate' (widely circulated) newspapers or journals in each State and the A.C.T., giving relevant information and inviting comment (normally within six weeks) from individuals who support or oppose the intended declaration.

The B.C.A. must consider all submissions regarding the intended declaration (section 18). If the B.C.A. decides (after consultation with A.A.C. and considering other information) 'that there is evidence that a person or the environment would be adversely affected' by biological control of the proposed target organism, 'but an adequate investigation or inquiry' into these effects has not been held, the B.C.A. can initiate one (or more) of three types of inquiry (section 19). Until the results of the inquiry (or inquiries) are known, the B.C.A. cannot take any further action on the recommendation to declare the organism as a target organism.

Inquiries

The three types of inquiry which may be called are: (1) under provision of Part VII; (2) under the *Industries Assistance Commission* (I.A.C.) *Act 1973* (Commonwealth of Australia 1973), arranged by the Minister responsible for the I.A.C., at the request of the B.C.A.; and (3) under the *Environment Protection (Impact of Proposals)* (E.P.I.P.) *Act 1974* (Commonwealth of Australia 1974), arranged by the Minister who administers this *Act*, at the request of the B.C.A.

(1) *Part VII Inquiry.* The B.C.A., in consultation with A.A.C., appoints one or more Commissioners to form the Commission of Inquiry, and can appoint one or more advisors (section 38). The Commission is directed to conduct an inquiry into matters that it feels necessary to investigate to determine if a potential program is in the national benefit, matters approved by the A.A.C., including whether assistance (compensation) should be given to persons if they are adversely affected by declaration of target or agent organisms, or any other matters it judges appropriate.

Commissioners are paid (section 39). Notice of inquiries are to be published in the *Gazette and* in newspapers or journals (section 40). Inquiries are conducted in public (except when it is in the public interest to hold them in private), results are to be made public (except in the case of confidential information or for 'any other reason' the Commission feels is suitable) (section 41), and the Commission is not bound by the rules of evidence. The Commission can summon witnesses, evidence is to be taken in public on oath or affirmation, etc. (sections 42–51),

Not being bound by the rules of evidence is important, and has positive and negative aspects. Essentially, this means that anecdotal evidence ('hearsay') can be presented. For example, a District Weeds Officer, Agronomist or similar person can report on the status of a weed in his or her District under this provision. If the Commission were to be bound by rules of evidence, each farmer in the District Weeds Officer's area of responsibility would have to report separately. This is a sensible and necessary provision, in that only a minimal number of witnesses need be called. However, it will allow presentation of unsubstantiated claims of varying quality about beneficial or detrimental aspects of a weed's status. The Commission could have a difficult job in evaluating such information. Similarly, unsubstantiated information concerning potential agent organisms during inquiries on the agents would require adjudication by the Commission.

(2) *I.A.C. Act 1973 Inquiry (subsections 19(f) and 28(f)).* Inquiries under this *Act* are conducted to enable the Temporary Assistance Authority (established by the Govenor-General to conduct inquiries under this *Act*) to determine the level of assistance (compensation) appropriate in a given case. The conduct of an inquiry under this *Act* is essentially the same as a Part VII inquiry.

(3) *E.P.I.P. Act 1974 Inquiry (subsections 19(g) and 28(g)).* Inquiries under this *Act* are conducted on environmental matters. The Minister administering this *Act* appoints one or more Commissioners and advisors. The conduct of an inquiry under this *Act* is essentially the same as a Part VII inquiry.

Declaration of target organisms (section 20). If the B.C.A. (after considering reports, results of an inquiry, etc.) is satisfied that the proposed organism is a pest in the A.C.T., and is controllable by biological control, and that control *throughout Australia* would not cause 'significant harm to any person or to the environment', or any harm so caused by successful biological control 'would be significantly less than the harm caused, or likely to be caused', by the organism in the absence of biological control, it shall declare the organism as a target organism by publishing a notice to that effect in the *Gazette*.

Agent Organisms (Part III)

The procedure leading to declaration of potential agent organisms (= biological control agents) is essentially identical to that for declaration of target organisms, except in one critical point. Action for declaration of potential agent organisms can be commenced by a recommendation to the B.C.A. by the A.A.C., or by application to the B.C.A. (as above) (sections 21 and 22). Applications can be withdrawn at any time up to referral to A.A.C. (section 23). Provisions for referral (or not) to A.A.C., rejection of applications, consideration of submissions, inquiries and declaration are similar to those covering target organisms (sections 24–5, 27–9).

The one critical point of difference between the procedure leading to declaration of agent organisms as compared to target organisms is in the level of advertising (section 26). Following a recommendation from B.C.A. to A.A.C. to declare the organisms as agent organisms, the B.C.A. is required to advertise the intent to declare only in the *Gazette*, not also in newspapers or journals (although the B.C.A. *may* also advertise in 'appropriate' newspapers or journals).

This notice in the *Gazette* still invites comment and could result in an inquiry *on each potential biological control agent* (section 28), in addition to the target organism. Also, the B.C.A. may set conditions on the release of agent organisms, such as who may release them, and circumstances in which they may be released (subsection 29(2)(a) and (b)). Both of these points are areas of significant potential problems (see below).

Other Provisions (Parts IV–VII)

If the B.C.A. is satisfied that an emergency situation exists that may be solvable by biological control (e.g. discovery of a new aphid species with the potential to become a major pest), it can declare by notice in the *Gazette* that pest to be a target organism and its specified natural enemies as agent organisms (section 30). Again, conditions can be specified as to who may release to agent organisms, and how they may be released.

The B.C.A. can declare by notice in the *Gazette* that previously released biological control agents are agent organisms, and the pests against which the agents were released are target organisms, if it is likely that they would have been so declared under the *Act* had it been in effect prior to release of agents (section 31). However, before such a declaration can be made, the B.C.A. may advertise in the *Gazette and* in newspapers or journals that it considers appropriate, that such declaration is being contemplated (section 32). As with other advertisements discussed above, persons are invited to comment on the proposal, and if necessary, the B.C.A. can call an inquiry (section 33).

A provision for reciprosity with relevant state laws is also included, and again, release conditions can be set (section 34).

Declared agent organisms for declared target organisms can be released in the field, following any conditions that may have been set (section 35). This represents legal approval for release, and is an important clause. Significantly, 'no action or other proceeding shall be instituted or continued in any court' to prevent release of declared agent organisms in the A.C.T., or to recover damages caused by their release, subject to certain conditions. For example, if a court order is in place preventing release of agent organisms in the A.C.T. (such as the perpetual injunction on the *Echium* program) it cannot be enforced (section 36). A similar section is included which covers State laws (section 37).

Four important points are contained in Part VIII of the *Act*. First, it is not compulsory to have target or agent organisms declared for a biological control program to be conducted (section 52); however, any program not so approved would, of course, be open to legal action. Second, the B.C.A. can revoke declaration of target organisms (and therefore agent organisms; there can be declared target organisms without declared agent organisms, but not vice versa) (section 53). Third, once declared, agent organisms can be released *in perpetuity*, unless declaration is revoked (section 54). Fourth, appeal provisions are included (section 56), covering many of the decisions detailed above.

Possible Remaining Problems

From the point of view of biological control research workers, some of the *Act*'s provisions have potential to cause several problems.

Advertising agent organisms. Some people contributing to the draft legislation felt that the requirement to advertise agents in the Government *Gazette*, and hence invite the possibility of an inquiry, would not impede biological control programs, because declarations of intent to declare potential target organisms and agent organisms can be made concurrently, and if an inquiry is needed, targets and agents can be investigated at the same time (section 28(2)). This, unfortunately, does not consider sufficiently the different nature of judgements over agents, and from a practical point of view would often be logistically impossible.

An alternative procedure discussed during the formulation of the *Act* was to leave the option of advertising each agent to the B.C.A. who would act on advice (essentially that of Plant Quarantine) for exotic agents for weeds. We feel this would have been preferable, in that questions of specificity and the possibility of damage to non-target species are essentially technical, and Plant Quarantine has a long history of successfully evaluating them. It seems unnecessary to advertise every agent organism (no matter how well researched) and invite comment and some further opportunities to elements of the community opposed to a declared program to further delay and hinder its implementation.

Naturally, if there is doubt over specificity and an evaluation is required of the relative merits of weed control and possible harm to other species, public advertisement and the possibility of inquiry is more necessary. This could also apply to use of indigenous species in inundative programs, over which Plant Quarantine has no control.

The dividing line between technical judgements (best made by competent scientists) and judgements of community implications (best made by the community) is always indistinct, but the decision to invite comment on all decisions, including the technical, could well yield further problems without compensating benefits.

From the point of view of timing, all potential biological control agents may not be known in sufficient detail at the time an inquiry is called to enable them to be proposed as agent organisms. This is the situation with the agents for *E. plantagineum*: of the 13 potential biological control agents (Wapshere 1984; Delfosse 1985), only eight are sufficiently well known in terms of safety (e.g. host range) to have them subjected to an inquiry (Delfosse, unpubl. data). Under the present conditions of the *Act*, a separate inquiry could be called for each species as testing is completed. This situation is typical for most weeds, so this provision could very well result in unreasonable delays and expense, without any increase in safety. The alternative is, of course, not to seek declarations of agents for declared weeds, but this could lead to other problems, particularly for programs with significant conflict of interest.

Past programs. This provision also appears unnecessary since programs that have been in operation over 60 years such as St. John's wort (*Hypericum perforatum* L.; Clusiaceae) or lantana (*Lantana camara* L.; Verbenacae), which have no detrimental aspects, would unwisely be open to challenge. The obvious course to follow for existing programs is not to apply for target or agent organism status.

Release conditions for agent organisms. The provisions in the *Act* to specify release conditions also seem unnecessary, and possibly inhibitory.

For a particular agent organism, generally only trained personnel (usually the people involved in mass-rearing the agent) who know the species well should release it. This is essentially an experimental procedure and could involve testing different methods, different times, different sites, etc. This is a scientific matter, and the investigator should have complete freedom to determine what is done, and how, when and by whom it is done. In fact, under provisions of the *Act* (section 35(2)), it would be illegal to release declared agent organisms 'otherwise than in accordance with those conditions'.

Conclusions

As pointed out by Andres (1981), for biological control programs to continue in situations where conflicts exist, it is firstly vital that mechanisms be found to get conflicting sides together, and secondly, that good information is available concerning the target weed and possible impact on non-target species.

This account has dealt with a legislative means of addressing the first point, or at least ensuring that all views are taken into account and a decision made — a system brought on largely by a massive breakdown in the previous consultative process. It is unfortunate that the *Act* was necessary, because it will certainly add to the cost (perhaps $100,000 p.a.; Commonwealth of Australia 1984*b*) and time-delays of implementing biological control.

Certain provisions of the *Act*, especially gazetting of potential biological control agents, could result in what should be scientific decisions, being made by lay people in a public forum.

The second point, that of providing good information, remains, and will continue to be a problem until researchers can provide better predictions of both the likely benefits from introductions in terms of effect on the target, and the possibilities of significant damage to non-target species.

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Note Added in Proof

On 26 October 1984, following assent to the *Biological Control Act 1984* on 25 October, Senator J.N. Button, then Minister for Industry and Commerce, referred the topic of 'whether *Echium* sp. ... should be a target for biological control' to the Industries Assistance Commission (IAC). The Biological Control Authority (BCA) also called an Inquiry on this subject in late December 1984 (Delfosse and Cullen 1985).

Initially, the IAC Final Report was due on 26 July 1985. However, about 600 submissions were made to these Inquiries, all of which had to be evaluated carefully by the IAC. As a result, the IAC sought, and obtained, an extension of the date of submission of their Final Report of the *Echium* Inquiry to 30 September 1985.

The IAC Draft Report of the *Echium* Inquiry was released on 25 July 1985 (IAC 1985). The Draft Report contained five draft recommendations: '(1) the Biological Control Authority declare *Echium* spp. a target for biological control; (2) the Biological Control Authority declare *Dialectica scalariella*, *Phytoecia coerulescens*, *Dictyla echii*, and *D. nassata* as control agents as soon as practicable, and declare *Ceutorhynchus geographicus*, *C. larvatus*, *Longitarsus aeneus* and *L. echii* as control agents subject to approval from the quarantine authorities; (3) CSIRO resume its program for biological control of *Echium* and, in conjunction with State governments, undertake release and monitoring of control agents; (4) no special adjustment assistance be made available at the time of implementation of biological control to those who might be adversely affected by biological control; and (5) the need and justification for any adjustment assistance be reviewed two years after implementation of biological control and if adjustment assistance is then seen as desirable, it be provided through the Rural Adjustment Scheme on the same terms as for other agricultural activities.'

Public hearings will be held on the IAC Draft Report at four locations in Australia during August 1985, and supplementary submissions can be lodged. However, in the Draft Report, the IAC found that there would be a 10.5:1 benefit:cost ratio in the first 15 years after implementation of a successful biological control program for *Echium* (total benefits, \$A155.1 million; total costs, \$A14.8 million; 5% discount rate after inflation), and that the ratio would become more favorable in succeeding years.

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Appendix 1

AUSTRALIA

Biological Control Act 1984

No. 139 of 1984

TABLE OF PROVISIONS

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Biological Control Act 1984

No. 139 of 1984

An Act to make provision for the biological control of pests in the Australian Capital Territory, and for related purposes

[*Assented to 25 October 1984*]

[*Date of commencement 22 November 1984*]

BE IT ENACTED by the Queen, and the Senate and the House of Representatives of the Commonwealth of Australia, as follows:

PART I—PRELIMINARY

Short title

1. This Act may be cited as the *Biological Control Act 1984*.

Interpretation

2. (1) In this Act, unless the contrary intention appears—

"agent application" means an application under section 22;

"agent recommendation" means a recommendation to the Authority by the Council that organisms of a particular kind should be declared to be agent organisms for the purposes of this Act;

"agent organisms" means organisms in respect of which there is in force a declaration by the Authority, under section 29, 30, 31 or 34, that the organisms are agent organisms for the purposes of this Act;

"Authority" means the Commonwealth Biological Control Authority established by section 8;

"Commonwealth Minister" or "the Minister" means the Minister for the time being administering this Act;

"control", in relation to organisms, includes—

- (a) reduce the number of those organisms;
- (b) prevent an increase in the number of those organisms;
- (c) reduce the activity or appetite of some or all of those organisms; and
- (d) modify the behaviour or characteristics of some or all of those organisms;

"Council" means the body known as the Australian Agricultural Council;

"kind", in relation to live organisms, means species, sub-species or variety;

"organism" means—

- (a) an organism (whether alive or dead and whether or not indigenous to Australia) other than man; or
- (b) a part of, or matter discharged from, an organism within the meaning of paragraph (a);

"organization" includes—

- (a) a body corporate;
- (b) an association or other body of persons; and
- (c) an association that consists of 2 or more organizations within the meaning of the preceding paragraphs;

"person" includes an organization;

"prescribed live organisms" means live organisms other than live vaccines or resistant cultivars;

"relevant State law" means a law of a State declared by the Authority under section 9 to be a relevant State law for the purposes of this Act;

"State" includes the Northern Territory;

"target application" means an application under section 13;

"target recommendation" means a recommendation to the Authority by the Council that organisms of a particular kind should be declared to be target organisms for the purposes of this Act;

"target organisms" means organisms in respect of which there is in force a declaration by the Authority, under section 20, 30, 31 or 34, that the organisms are target organisms for the purposes of this Act;

"Territory" does not include the Northern Territory.

(2) For the purposes of this Act, the Jervis Bay Territory shall be taken to be part of the Australian Capital Territory.

(3) For the purposes of this Act, organisms of a particular kind shall be taken to cause harm if the control of those organisms would be for the public benefit.

(4) For the purposes of this Act, organisms of a particular kind shall be taken to cause harm in the Australian Capital Territory if they cause harm in a part or parts only of that Territory.

(5) A reference in this Act to a recommendation by the Council that organisms of a particular kind should be declared to be agent organisms for the purposes of this Act includes a reference to a recommendation that organisms of a particular kind should be so declared if organisms to which a target recommendation applies are declared to be target organisms for the purposes of this Act.

(6) In this Act—

(a) a reference to a Minister of a State shall, except in relation to the Northern Territory, be read as a reference to a Minister of the Crown of the State; and

(b) a reference to a Minister of a State shall, in relation to the Northern Territory, be read as a reference to a person holding an office referred to in section 34 of the *Northern Territory (Self-Government) Act 1978*.

Biological control

3. For the purposes of this Act, organisms of a particular kind shall be taken to be controllable by biological means if, and only if, those organisms can be controlled by the release of live organisms of another kind.

Extension of Act to external Territories

4. (1) The Minister may, by notice published in the *Gazette*, declare that this Act extends to—

(a) the Territory of Cocos (Keeling) Islands;

(b) the Territory of Christmas Island;

(c) the Coral Sea Islands Territory; or

(d) the Territory of Ashmore and Cartier Islands.

(2) Where a declaration under sub-section (1) is in force in relation to a Territory, this Act has effect, in relation to that Territory, as if the references in this Act, other than in this section, to the Australian Capital Territory were references to that Territory.

Saving of other laws

5. (1) This Act shall be read and construed as being in addition to, and not in derogation of or in substitution for—

(a) any other law of the Commonwealth, whether passed or made before or after the commencement of this Act; or

(b) if this Act extends to an external Territory, any law of that Territory, whether passed or made before or after the commencement of this Act.

(2) Without limiting the generality of sub-section (1), this Act shall not be read or construed as authorizing or permitting the doing of any act in contravention of—

(a) the *Quarantine Act 1908*; or

(b) the *Wildlife Protection (Regulation of Exports and Imports) Act 1982.*

Act to bind Crown

6. (1) This Act binds the Crown in right of the Commonwealth, of each of the States and of Norfolk Island.

(2) Nothing in this Act renders the Crown in right of the Commonwealth, of a State or of Norfolk Island liable to be prosecuted for an offence.

Act not limited to agricultural pests

7. The fact that certain powers of the Authority under this Act cannot be exercised except on the recommendation of the Council does not imply that the only kinds of organisms that may be regarded as causing harm for the purposes of this Act are kinds that are harmful by reason of their effect on agriculture.

Commonwealth Biological Control Authority

8. (1) For the purposes of this Act, a Commonwealth Biological Control Authority is established by this section.

(2) From the commencement of this Act until 1 April 1985 the Authority shall be constituted by the Commonwealth Minister.

(3) Before 1 April in each year, the Commonwealth Minister, after consultation with the Council, shall, in writing, designate either the Commonwealth Minister, or the Minister of a State who is administering a relevant State law, as the Authority for the year commencing on that day and, subject to sub-section (4), during that year, the Authority shall be constituted by the Minister so designated.

(4) If, during a year for which a Minister of a State is designated as the Authority, there ceases to be a law of that State that is a relevant State law, the Authority shall cease to be constituted by that Minister and the Authority shall, for the balance of that year, be constituted by the Commonwealth Minister.

(5) Where—

(a) the Authority is constituted by the Commonwealth Minister; and

(b) another Minister of the Commonwealth is for the time being acting for and on behalf of the Commonwealth Minister,

a reference in this Act, other than in this section, to the Authority shall be read as including a reference to that other Minister.

(6) Where—

(a) the Authority is constituted by a Minister of a State; and

(b) another Minister of that State is for the time being acting for and on behalf of the first-mentioned Minister, a reference in this Act, other than in this section, to the Authority shall be read as including a reference to that other Minister.

Relevant State laws

9. Where a law of a State—

(a) provides for the control by biological means of organisms causing harm in the State;

(b) establishes an authority having similar powers and functions to those of the Authority; and

(c) contains provisions by virtue of which the authority so established and the Authority are constituted at all times by the same person,

the Authority may, by notice published in the *Gazette*, declare that law to be a relevant State law for the purposes of this Act.

Delegation

10. **(1)** The Authority may, either generally or as otherwise provided by the instrument of delegation, by writing signed by the Authority, delegate to an officer of the Department any of the powers of the Authority under this Act, other than—

(a) the powers of the Authority under section 9, 19, 20, 28, 29, 30, 31, 33, 34, 38 or 53; or

(b) this power of delegation.

(2) A power so delegated, when exercised by the delegate, shall, for the purposes of this Act, be deemed to have been exercised by the Authority.

(3) A delegation under this section does not prevent the exercise of a power by the Authority.

Operation of Industries Assistance Commission Act

11. Without limiting the generality of paragraph 4 (2) (a) of the *Industries Assistance Commission Act 1973*, for the purposes of that Act—

(a) a declaration that organisms of a particular kind that have an adverse effect on the carrying on by a person of a business or activity are target organisms for the purposes of this Act; or

(b) a declaration that organisms of another kind the release of which could control the population of organisms of the first-mentioned kind are agent organisms for the purposes of this Act,

shall be taken to be assistance by way of the doing of an act that would assist that person to carry on that business or activity.

PART II—TARGET ORGANISMS

Target organisms

12. **(1)** Subject to and in accordance with this Part, organisms of a particular kind may be declared to be target organisms for the purposes of this Act.

(2) Action for the declaration of target organisms in accordance with this Part may be commenced by—

(a) a recommendation to the Authority by the Council; or

(b) an application under section 13.

Target application

13. (1) Where a person considers that organisms of a particular kind are causing harm in the Australian Capital Territory and are, or are likely to be, controllable by biological means, the person may make an application to the Authority for a declaration that organisms of that kind are target organisms for the purposes of this Act.

(2) A target application shall be in writing signed—

(a) in the case of an application by a natural person—by the applicant; or

(b) in any other case—by a natural person authorized by the applicant to do so.

(3) A target application in relation to organisms of a particular kind shall set out—

(a) particulars identifying the organisms;

(b) particulars of the reasons why the organisms are considered to be causing harm in the Australian Capital Territory;

(c) reasons why the applicant considers that the organisms are, or are likely to be, controllable by biological means; and

(d) such other particulars (if any) as are prescribed.

Withdrawal of target application

14. (1) A person who has made a target application may withdraw that application at any time before the application is referred to the Council under sub-section 15 (1).

(2) The withdrawal of a target application is to be effected by the making of a request for withdrawal to the Authority in writing signed—

(a) in the case of an application by a natural person—by the person who signed the application or by the legal personal representative of that person; or

(b) in any other case—by the person who signed the application or by a person authorized by the applicant to sign the request.

Referral of target application to Council

15. (1) Subject to sub-section (2), where a target application is received by the Authority, the Authority shall refer the application to the Council for its consideration.

(2) The Authority is not required to refer to the Council a target application in respect of organisms of a particular kind if—

(a) other action to have them declared to be target organisms is being, or has been, taken under this Act; or

(b) action to have them declared to be organisms that may be controlled by biological means is being, or has been, taken under a relevant State law.

Notice of rejection of target application

16. (1) If the Council, after considering a target application referred to it by the Authority, informs the Authority that it does not recommend that the organisms to which the application relates should be target organisms, the Authority shall cause to be given, in such manner as the Authority considers appropriate, to the person who made the target application and to the persons (if any) who made a later target application in respect of those organisms notice in writing stating that the Council does not recommend that those organisms should be target organisms.

(2) A notice under sub-section (1) shall—

(a) if reasons have been given by the Council for not recommending that organisms to which the notice relates should be target organisms—set out those reasons; and

(b) if there are circumstances in which, in the opinion of the Authority, a target application in relation to those organisms might result in a recommendation by the Council that those organisms should be target organisms—specify those circumstances.

Notice of proposed target organisms

17. (1) Where the Council has recommended to the Authority that organisms of a particular kind should be target organisms the Authority shall publish in the *Gazette* and in such newspapers or journals as the Authority considers appropriate a notice that the Authority is contemplating declaring those organisms to be target organisms.

(2) Without limiting the generality of sub-section (1), a notice under that sub-section shall be published in each State and the Australian Capital Territory by being published in at least one newspaper circulating generally in that State or Territory.

(3) A notice under sub-section (1) in relation to organisms of a particular kind shall—

(a) set out particulars identifying the organisms;

(b) set out brief particulars of the reasons why the organisms are believed to be causing harm in the Australian Capital Territory;

(c) set out brief particulars of the benefits (if any) resulting from the absence of biological control of the population of the organisms;

(d) state that the Council has recommended that the organisms should be declared to be target organisms;

(e) where the recommendation of the Council followed a target application in relation to the organisms—inform the public that copies of the target application can be perused at a place specified in the notice; and

(f) invite any persons who object to, or support, the organisms being declared to be target organisms to submit written particulars of the grounds for that objection or support, as the case may be, to the Authority within the period of 6 weeks after the date of the publication of the notice in the *Gazette*, or within such further period as the Authority (either before or after the expiration of that period) allows.

(4) Where the Authority publishes a notice under sub-section (1) in relation to a target application, the Authority shall cause copies of the application to be available for perusal at the place specified in the notice in accordance with paragraph (3) (e).

Consideration of submissions relating to target organisms

18. The Authority shall consider any submissions in response to an invitation referred to in paragraph 17 (3) (f).

Inquiries relating to target organisms

19. **(1)** Where the Authority, after—

(a) complying with sections 17 and 18 in respect of a target recommendation;

(b) consulting the members of the Council regarding the appropriateness of action under this section in respect of that recommendation;

(c) considering the nature of, the proceedings in, and the findings of, any inquiry that the Authority considers relevant to the recommendation (which may be an inquiry conducted on behalf of a State); and

(d) considering any reports relating to the recommendation made by any person or authority competent to do so that the Authority considers relevant,

considers that there is evidence that a person or the environment would be adversely affected by the control of organisms of the kind to which the recommendation relates but an adequate investigation or inquiry into the effect of such control has not been held, the Authority may—

(e) direct that an inquiry under Part VII be conducted in respect of the recommendation;

(f) where the Authority considers it appropriate to do so, arrange for the Minister who administers the *Industries Assistance Commission Act 1973* to refer the recommendation to the Industries Assistance Commission for inquiry and report; or

(g) where the Authority considers it appropriate to do so, arrange for the Minister who administers the *Environment Protection (Impact of Proposals) Act 1974* to direct that an inquiry be conducted under that Act in respect of the recommendation.

(2) Where the Authority takes action under paragraph (1) (e), (f) or (g) for an inquiry in relation to a target recommendation, the Authority shall not take any further action under this Act in relation to that recommendation unless and until the Authority has considered the report made as the result of that inquiry.

Declaration of target organisms

20. **(1)** Where the Authority, after—

(a) complying with the preceding provisions of this Part in relation to a target recommendation; and

(b) considering all reports and other matters relating to that recommendation that the Authority considers it appropriate to consider,

is satisfied—

(c) that organisms of the kind to which the recommendation relates are causing harm in the Australian Capital Territory;

(d) that organisms of that kind are, or that there is a probability that organisms of that kind are likely to be, controllable by biological means; and

(e) that—

(i) the control throughout Australia of organisms of that kind would not cause any significant harm to any person or to the environment; or

(ii) any harm caused to persons or to the environment by the control throughout Australia of organisms of that kind would be significantly less than the harm caused, or likely to be caused, by failure to control organisms of that kind throughout Australia,

the Authority shall, by notice published in the *Gazette*, declare organisms of that kind to be target organisms for the purposes of this Act.

(2) In paragraph (1) (e), "Australia" includes the external Territories (if any) in respect of which a declaration under sub-section (1) is in force.

PART III—AGENT ORGANISMS

Agent organisms

21. **(1)** Subject to and in accordance with this Part, prescribed live organisms of a particular kind may be declared to be agent organisms for the purposes of this Act.

(2) Action for the declaration of agent organisms in accordance with this Part may be commenced by—

(a) a recommendation made to the Authority by the Council; or

(b) an application under section 22.

Agent application

22. **(1)** Where a person considers that the release of prescribed live organisms of a particular kind would result in the control of—

(a) target organisms of a particular kind or kinds; or

(b) organisms to which a target recommendation applies or target recommendations apply,

(whether or not the organisms referred to in paragraph (a) or (b) can be controlled by existing agent organisms) the person may make an application to the Authority for a declaration that the first-mentioned organisms are agent organisms for the purposes of this Act.

(2) An agent application shall be in writing signed—

(a) in the case of an application by a natural person—by the applicant; or

(b) in any other case—by a natural person authorized by the applicant to do so.

(3) An agent application in relation to organisms of a particular kind shall set out—

(a) particulars identifying the organisms;

(b) particulars of the possible ways in which the applicant considers that the release of the organisms could control the relevant population of target organisms; and

(c) such other particulars (if any) as are prescribed.

Withdrawal of agent application

23. **(1)** A person who has made an agent application may withdraw that application at any time before the application is referred to the Council under sub-section 24 (1).

(2) The withdrawal of an agent application is to be effected by the making of a request for withdrawal to the Authority in writing signed—

(a) in the case of an application by a natural person—by the person who signed the application or by the legal personal representative of that person; or

(b) in any other case—by the person who signed the application or by a person authorized by the applicant to sign the request.

Referral of agent application to Council

24. **(1)** Subject to sub-section (2), where an agent application is received by the Authority, the Authority shall refer the application to the Council for its consideration.

(2) The Authority is not required to refer to the Council an agent application in respect of organisms of a particular kind if—

(a) other action to have them declared to be agent organisms is being, or has been, taken under this Act; or

(b) action to have them declared to be organisms that may be released to control the population of other organisms is being, or has been, taken under a relevant State law.

Notice of rejection of agent application

25. **(1)** If the Council, after considering an agent application referred to it by the Authority, informs the Authority that it does not recommend that the organisms to which the application relates should be agent organisms, the Authority shall cause to be given, in such manner as the Authority considers appropriate, to the person who made the agent application and to the persons (if any) who made a later agent application in respect of those organisms notice in writing that the Council does not recommend that those organisms should be agent organisms.

(2) A notice under sub-section (1) shall—

(a) if reasons have been given by the Council for not recommending that organisms to which the notice relates should be agent organisms—set out those reasons; and

(b) if there are circumstances in which, in the opinion of the Authority, an agent application in relation to those organisms might result in a recommendation by the Council that those organisms should be agent organisms—specify those circumstances.

Notice of proposed agent organisms

26. **(1)** Where the Council has recommended to the Authority that prescribed live organisms of a particular kind should be agent organisms, the Authority shall publish in the *Gazette*, and may publish in such newspapers or journals as the Authority thinks appropriate, a notice that the Authority is contemplating declaring those organisms to be agent organisms.

(2) A notice under sub-section (1) in relation to organisms of a particular kind (in this sub-section referred to as the "relevant organisms") shall—

(a) set out particulars identifying the relevant organisms;

(b) specify the organisms which it is intended to control by the release of the relevant organisms;

(c) set out brief particulars of the manner in which the relevant organisms would control the organisms specified in the notice in accordance with paragraph (b);

(d) state that the Council has recommended that the relevant organisms should be declared to be agent organisms;

(e) where the recommendation of the Council followed an agent application in relation to the organisms—inform the public that copies of the agent application can be perused at a place specified in the notice; and

(f) invite any persons who object to, or support, the relevant organisms being declared to be agent organisms to submit written particulars of the grounds for that objection or support, as the case may be, to the

Authority within the period of 6 weeks after the date of the publication of the notice in the *Gazette*, or within such further period as the Authority (either before or after the expiration of that period) allows.

(3) Where the Authority publishes a notice under sub-section (1) in relation to an agent application, the Authority shall cause copies of the application to be available for perusal at the place specified in the notice in accordance with paragraph (2) (e).

(4) Where the Council has recommended to the Authority that 2 or more kinds of organisms should be agent organisms for the purpose of the control of the same population of particular organisms, a notice under sub-section (1) relating to one of those kinds may be combined with a notice under that sub-section relating to the other kind.

Consideration of submissions relating to agent organisms

27. The Authority shall consider any submissions in response to an invitation referred to in paragraph 26 (2) (f).

Inquiries relating to agent organisms

28. (1) Where the Authority, after—

(a) complying with sections 26 and 27 in respect of an agent recommendation;

(b) consulting the members of the Council regarding the appropriateness of action under this section in respect of that recommendation;

(c) considering the nature of, the proceedings in, and the findings of, any inquiry that the Authority considers relevant to the recommendation (which may be an inquiry under Part VII in respect of a target recommendation or an inquiry conducted on behalf of a State); and

(d) considering any reports relating to the recommendation made by any person or authority competent to do so that the Authority considers relevant,

considers that there is evidence that a person or the environment would be adversely affected by the release of organisms of the kind to which the recommendation relates but an adequate investigation or inquiry into the effect of such a release has not been held, the Authority may—

(e) direct that an inquiry under Part VII be conducted in respect of the recommendation;

(f) where the Authority considers it appropriate to do so, arrange for the Minister who administers the *Industries Assistance Commission Act 1973* to refer the recommendation to the Industries Assistance Commission for inquiry and report; or

(g) where the Authority considers it appropriate to do so, arrange for the Minister who administers the *Environment Protection (Impact of Proposals) Act 1974* to direct that an inquiry be conducted under that Act in respect of the recommendation.

(2) An inquiry by virtue of paragraph (1) (e), (f) or (g) in respect of an agent recommendation that recommends that organisms of a particular kind should be declared to be agent organisms if organisms to which a target recommendation applies are declared to be target organisms and an inquiry by virtue of paragraph 19 (1) (e), (f) or (g), as the case may be, in respect of that target recommendation may be conducted as if they were one inquiry.

(3) Where the Authority takes action under paragraph (1) (e), (f) or (g) for an inquiry in relation to an agent recommendation, the Authority shall not take any further action under this Act in relation to that recommendation unless and until the Authority has considered the report made as the result of that inquiry.

Declaration of agent organisms

29. **(1)** Where the Authority, after—

(a) complying with the preceding provisions of this Part in relation to an agent recommendation; and

(b) considering all reports and other matters relating to that recommendation that the Authority considers it appropriate to consider,

is satisfied—

(c) that the release of organisms of the kind to which the recommendation relates (in this sub-section referred to as the "relevant organisms") could result in the control of target organisms of a particular kind or kinds in the Australian Capital Territory; and

(d) that—

  (i) the release of the relevant organisms would not cause any significant harm to any person or to the environment, other than the harm (if any) resulting from the control throughout Australia of target organisms of that kind or those kinds; or

  (ii) any harm caused to persons or to the environment by the release of the relevant organisms, other than the harm (if any) resulting from the control throughout Australia of target organisms of that kind or those kinds, would be significantly less than—

    (A) the harm caused, or likely to be caused, by failure to control target organisms of that kind or those kinds throughout Australia; and

    (B) where target organisms of that kind or those kinds can be controlled by the release of other organisms or otherwise than by biological means—the harm (if any) caused, or likely to be caused, by controlling target organisms of that kind or those kinds throughout Australia by the release of those other organisms or by those other means, the Authority shall, by notice published in the *Gazette*, declare the relevant organisms to be agent organisms for the purposes of this Act.

(2) A notice under sub-section (1) declaring organisms of a particular kind to be agent organisms may set out conditions under which those organisms may be released, which conditions may be or include—

(a) conditions specifying the persons who may release those organisms; or

(b) conditions specifying the circumstances in which those organisms may be released.

(3) In paragraph (1) (d), "Australia" has the same meaning as it has in paragraph 20 (1) (e).

PART IV—SPECIAL DECLARATIONS OF TARGET ORGANISMS AND AGENT ORGANISMS

Emergency declarations

30. **(1)** If the Authority is satisfied—

(a) that an emergency exists because organisms of a particular kind (whether or not they are target organisms)—

  (i) are having, or are likely to have, a serious effect on the health of humans, animals or plants in the Australian Capital Territory;

  (ii) are causing, or are likely to cause, harm in that Territory so as to result in significant damage to the economy; or

  (iii) are causing, or are likely to cause, significant damage to the environment in that Territory;

(b) that the release of prescribed live organisms that are not agent organisms would control the first-mentioned organisms; and

(c) the release of the organisms of the second-mentioned kind would not have any significant adverse effects,

the Authority shall, by notice published in the *Gazette*, declare—

(d) where the organisms of the first-mentioned kind are not target organisms, the organisms of the first-mentioned kind to be target organisms for the purposes of this Act; and

(e) organisms of the second-mentioned kind to be agent organisms for the purposes of this Act.

(2) A notice under sub-section (1) declaring organisms of a particular kind to be agent organisms may set out particulars of the conditions under which those organisms may be released, which conditions may be or include—

(a) conditions specifying the persons who may release those organisms; or

(b) conditions specifying the circumstances in which those organisms may be released.

Declarations of existing released organisms

31. **(1)** If the Authority is satisfied that—

(a) before the commencement of this Act, prescribed live organisms of a particular kind were released in the Australian Capital Territory for the purpose of the control, by biological means, of organisms of another kind in that Territory; and

(b) if this Act had been in force before the release of the first-mentioned organisms, it is probable that action would have been taken under this Act that would have resulted in the organisms of the second-mentioned kind being declared to be target organisms and the organisms of the first-mentioned kind being declared to be agent organisms,

the Authority may, by notice published in the *Gazette*, declare—

(c) organisms of the second-mentioned kind to be target organisms for the purposes of this Act; and

(d) organisms of the first-mentioned kind to be agent organisms for the purposes of this Act.

(2) A notice under sub-section (1) declaring organisms of a particular kind to be agent organisms may set out conditions under which the organisms may be released, which conditions may be or include—

(a) conditions specifying the persons who may release those organisms; or

(b) conditions specifying the circumstances in which those organisms may be released.

Notice of proposed declaration under section 31

32. **(1)** Where the Authority is contemplating making a declaration under section 31, the Authority may publish in the *Gazette* and in such newspapers or journals as the Authority considers appropriate a notice that the Authority is contemplating making that declaration.

(2) A notice under sub-section (1) shall—

(a) set out particulars identifying the organisms that the Authority is contemplating declaring to be target organisms;

(b) set out particulars identifying the organisms that the Authority is contemplating declaring to be agent organisms;

(c) identify the occasions known to the Authority on which the organisms referred to in paragraph (b) were released; and

(d) invite any persons who object to, or support, the declaration being made to submit written particulars of the grounds for that objection or support, as the case may be, to the Authority within 6 weeks after the date of the publication of the notice in the *Gazette*, or within such further period as the Authority (either before or after the expiration of that period) allows.

(3) Where the Authority publishes a notice under sub-section (1) in relation to a contemplated declaration, the Authority shall not make that declaration unless and until the Authority has considered any submissions in response to an invitation referred to in paragraph (2) (d) in relation to the declaration.

Inquiries relating to declarations under section 31

33. **(1)** Where the Authority—

(a) is contemplating making a declaration under section 31; and

(b) after—

   (i) consulting the members of the Council regarding the appropriateness of action under this section in respect of the contemplated declaration;

   (ii) considering the nature of, the proceedings in, and the findings of, any inquiry that the Authority considers relevant (which may be an inquiry conducted on behalf of a State); and

   (iii) considering any reports made by any person or authority competent to do so that the Authority considers relevant,

considers that there is evidence that a person or the environment would be adversely affected by the release of organisms of the kind to which the declaration would relate but an adequate investigation or inquiry into the effect of such a release has not been held,

the Authority may—

(c) direct that an inquiry under Part VII be conducted in respect of the contemplated declaration;

(d) where the Authority considers it appropriate to do so, arrange for the Minister who administers the *Industries Assistance Commission Act 1973* to refer the contemplated declaration to the Industries Assistance Commission for inquiry and report; or

(e) where the Authority considers it appropriate to do so, arrange for the Minister who administers the *Environment Protection (Impact of Proposals) Act 1974* to direct that an inquiry be conducted under that Act in respect of the contemplated declaration.

(2) Where the Authority takes action under paragraph (1) (c), (d) or (e) for an inquiry in relation to a contemplated declaration, the Authority shall not make that declaration unless and until the Authority has considered the report made as the result of the inquiry.

Declaration of organisms declared under relevant State law

34. **(1)** Where organisms of a particular kind are organisms that for the purposes of a relevant State law may be controlled by biological means, the Authority may, by notice published in the *Gazette*, declare those organisms to be target organisms for the purposes of this Act.

(2) Where—

(a) prescribed live organisms of a particular kind are organisms that for the purposes of a relevant State law may be released to control other organisms; and

(b) those other organisms are target organisms, the Authority shall, by notice published in the *Gazette*, declare those first-mentioned organisms to be agent organisms for the purposes of this Act.

(3) A notice under sub-section (2) declaring organisms of a particular kind to be agent organisms may set out conditions under which the organisms may be released, which conditions may be or include—

(a) conditions specifying the persons who may release those organisms; or

(b) conditions specifying the circumstances in which those organisms may be released.

PART V—RELEASE OF AGENT ORGANISMS

Release of agent organisms

35. (1) Subject to sub-section (2), agent organisms may be released in the Australian Capital Territory.

(2) Where a notice under section 29, 30, 31 or 34 declaring organisms to be agent organisms specified conditions under which the organisms may be released, those organisms shall not be released otherwise than in accordance with those conditions.

No legal proceedings to be instituted in respect of release of agent organisms

36. (1) Subject to sub-section (3), no action or other proceeding shall be instituted or continued in any court—

(a) to prevent the release of agent organisms in accordance with section 35;

(b) to recover damages in respect of any loss incurred, or any damage suffered, in a Territory by reason of the release of agent organisms in accordance with that section; or

(c) to recover damages in respect of any loss incurred, or any damage suffered, in a State by reason of the release of agent organisms in accordance with that section.

(2) If, at the time at which organisms of a particular kind were declared under section 29, 30, 31 or 34 to be agent organisms, there was in force an order of a court relating to the release of organisms of that kind, no action or other proceeding shall be instituted or continued in any court in respect of that order in so far as the order purports to prohibit a person from—

(a) releasing organisms of that kind in the Australian Capital Territory in accordance with section 35; or

(b) doing anything to assist or further the release of organisms of that kind in that Territory in accordance with section 35.

(3) Nothing in sub-section (1) prevents the institution or continuation in any court of an action or other proceeding to recover damages in respect of any loss incurred, or any damage suffered, by reason of the release of agent organisms of a particular kind in accordance with section 35 where—

(a) the loss incurred or the damage suffered was the result of the release having had a significant effect on other organisms;

(b) at the time of the release, the persons in Australia having a reputation for special knowledge of the biology of organisms of that kind knew, or had reasonable grounds to expect, that such a release could have such an effect; and

(c) in making the declaration declaring organisms of that kind to be agent organisms, the Authority did not take into account (whether because of the state of scientific knowledge or otherwise) the factor that such a release could have such an effect.

PART VI—BIOLOGICAL CONTROL UNDER STATE LAWS

Legal proceedings not to be instituted

37. **(1)** Subject to sub-section (4), no action or other proceeding shall be instituted or continued in any court to recover damages in respect of any loss incurred, or any damage suffered, in a Territory by reason of the release of organisms in accordance with a relevant State law.

(2) Subject to sub-section (4), no action or other proceeding shall be instituted or continued in any court of a Territory—

(a) to prevent the release of organisms in accordance with a relevant State law; or

(b) to recover damages in respect of any loss incurred, or any damage suffered, in a State by reason of the release of organisms in accordance with a relevant State law.

(3) If, at the time at which prescribed live organisms of a particular kind became organisms that could be released in accordance with a relevant State law, there was in force an order of a court relating to the release of organisms of that kind, no action or other proceeding shall be instituted or continued in any court of a Territory in respect of that order in so far as the order purports to restrict a person from—

(a) releasing organisms of that kind in accordance with that law; or

(b) doing anything to assist or further the release of organisms of that kind in accordance with that law.

(4) Nothing in sub-section (1) or (2) prevents the institution or continuation in any court of an action or other proceeding to recover damages in respect of any loss incurred, or any damage suffered, by reason of the release of organisms of a particular kind in accordance with a relevant State law where—

(a) the loss incurred or the damage suffered was the result of the release having had a significant effect on other organisms;

(b) at the time of the release, the persons in Australia having a reputation for special knowledge of the biology of organisms of that kind knew, or had reasonable grounds to expect, that such a release could have such an effect; and

(c) in making the declaration by virtue of which organisms of that kind became organisms that could be released in accordance with the relevant State law, the authority established by that law did not take into account (whether because of the state of scientific knowledge or otherwise) the factor that such a release could have such an effect.

PART VII—INQUIRIES

Commissions of inquiry

38. **(1)** Where, in accordance with paragraph 19 (1) (e), 28 (1) (e) or 33 (1) (c), the Authority directs that an inquiry be conducted under this Part, the Authority shall, after consulting the members of the Council, appoint a Commissioner or Commissioners to be a Commission to conduct that inquiry and may appoint a person or persons to advise the Commission.

(2) Where there is more than one Commissioner, the Authority shall appoint one of the Commissioners to preside at the inquiry.

(3) A Commission established to conduct an inquiry shall inquire into—

(a) such matters as it considers necessary to ascertain, from the broad community viewpoint, the overall benefits and disadvantages of declaring organisms of the kind to which the inquiry relates to be target organisms or agent organisms, as the case requires;

(b) such relevant matters approved by the Council as the Authority, by notice in writing given to the Commissioner or to the Commissioner presiding at the inquiry, as the case requires, directs, which may be or include the following matter, namely, whether assistance should be given to any persons if a declaration is made in respect of those organisms; and

(c) any other relevant matters that the Commission considers it should inquire into.

(4) The Commission shall report its findings and recommendations to the Authority and shall, after so reporting but subject to sub-section (6), make public those findings and recommendations.

(5) When the Authority appoints a Commissioner or Commissioners to be a Commission, the Authority may nominate a day as the day on which the Commission is to report its findings and recommendations to the Authority, and, where the Authority nominates a day, the Commission shall report its findings and recommendations to the Authority on or before that day or such later day as the Authority (before the nominated day) allows.

(6) The Commission shall not make public any evidence or matters in respect of which directions have been given under paragraph 41 (2) (b) or matters the publication of which is excepted from sub-section 41 (5).

(7) Subject to this Act, a Commission is not subject to directions by the Authority, or otherwise by or on behalf of the Government of the Commonwealth, in or in relation to the conduct of an inquiry.

Remuneration of Commissioners

39. (1) A Commissioner shall be paid such remuneration as is determined by the Remuneration Tribunal, but, if no determination of that remuneration by the Tribunal is in operation, he shall be paid such remuneration as is prescribed.

(2) A Commissioner shall be paid such allowances as are prescribed.

(3) This section has effect subject to the *Remuneration Tribunals Act 1973.*

Notice of inquiries

40. Before a Commission commences an inquiry, the Commission shall give reasonable notice, by advertisement published in the *Gazette* and in such newspapers or journals as it thinks necessary, of its intention to hold the inquiry, the subject of the inquiry and the time and place at which the inquiry is to be commenced.

Procedure at inquiries

41. (1) Subject to this section, an inquiry by a Commission shall be held in public and evidence in the inquiry shall be taken in public on oath or affirmation.

(2) Where a Commission is satisfied that it is desirable to do so in the public interest by reason of the confidential nature of any evidence or matter or for any other reason, the Commission may—

(a) direct that an inquiry or a part of an inquiry shall take place in private and give directions as to the persons who may be present; or

(b) give directions prohibiting or restricting the publication of evidence given before the Commission or of matters contained in documents lodged with the Commission.

(3) A Commission may, if it thinks fit, permit a person appearing as a witness before the Commission to give evidence by tendering, and verifying by oath or affirmation, a written statement.

(4) Where a Commission considers that the attendance of a person as a witness before the Commission would cause serious hardship to a person, the Commission may permit the person to give evidence by sending to the Commission a written statement, verified in such manner as the Commission allows.

(5) Where evidence is given to a Commission by a written statement in accordance with sub-section (3) or (4), the Commission shall make available to the public in such manner as the Commission thinks fit the contents of the statement other than any matter the publication of which, in the opinion of the Commission, would be contrary to the public interest by reason of its confidential nature or for any other reason.

(6) Subject to this section and the regulations—

(a) the procedure to be followed at an inquiry by a Commission is within the discretion of the Commission; and

(b) a Commission is not bound by the rules of evidence.

Power to summon witnesses

42. A Commissioner may, by writing signed by the Commissioner, summon a person to appear before the Commission at a time and place specified in the summons to give evidence and produce such books and documents (if any) as are referred to in the summons.

Failure of witness to attend

43. A person served with a summons to appear as a witness at an inquiry by a Commission shall not, without reasonable excuse—

(a) fail to attend as required by the summons; or

(b) fail to appear and report himself or herself from day to day unless excused or released from further attendance by or on behalf of the Commission.

Penalty: $1,000 or imprisonment for 6 months, or both.

Power to administer oath or affirmation

44. A Commissioner may administer an oath or affirmation to a person appearing as a witness before the Commission.

Refusal to be sworn or to answer questions

45. A person appearing as a witness at an inquiry by a Commission shall not, without reasonable excuse—

(a) refuse or fail to be sworn or to make an affirmation; or

(b) refuse or fail to answer a question that the person is required to answer by the Commissioner presiding at the inquiry; or

(c) refuse or fail to produce a document that the person was required to produce by a summons under this Act served on him.

Penalty: $1,000 or imprisonment for 6 months, or both.

Protection of Commissioners and witnesses

46. (1) A Commissioner has, in the performance of the duties of a Commissioner, the same protection and immunity as a Justice of the High Court.

(2) Subject to this Act, a person appearing before a Commission as a witness at an inquiry has the same protection, and is, in addition to the penalties provided by this Act, subject to the same liabilities, in any civil or criminal proceedings as a witness in proceedings in the High Court.

False or misleading evidence

47. (1) A person shall not, at a hearing before a Commission, give evidence that is to the knowledge of the person false or misleading in a material particular.

(2) An offence against sub-section (1) is an indictable offence and, subject to this section, is punishable, upon conviction, by imprisonment for a period not exceeding 2 years or by a fine not exceeding $5,000, or both.

(3) Notwithstanding that an offence against sub-section (1) is an indictable offence, a court of summary jurisdiction may hear and determine proceedings in respect of such an offence if the court is satisfied that it is proper to do so and the defendant and the prosecutor consent.

(4) Where, in accordance with sub-section (3), a court of summary jurisdiction convicts a person of an offence against sub-section (1), the penalty that the court may impose is a fine not exceeding $2,000 or imprisonment for a period not exceeding one year, or both.

Contempt of Commission

48. (1) A person shall not—

(a) obstruct or hinder a Commission or a Commissioner in the conduct of an inquiry; or

(b) disrupt a hearing before a Commission.

Penalty: $2,000 or imprisonment for one year, or both.

(2) An offence against sub-section (1) is punishable on summary conviction.

Powers of Commission in relation to documents produced

49. (1) A Commissioner, or a person assisting a Commission and authorized by a Commissioner to do so, may inspect any books or documents furnished to the Commission for the purposes of the performance of its functions under this Act or produced at an inquiry and may make copies of, or take extracts from, those books or documents.

(2) Books or documents so furnished may be retained by the Commission for such reasonable period as the Commission thinks fit.

Allowances to witnesses

50. A witness summoned under this Act to appear at an inquiry by a Commission is entitled to be paid by the Commonwealth such allowances for the witness's travelling and other expenses as are prescribed.

Witness not to be prejudiced

51. **(1)** A person shall not—

(a) use violence to or inflict injury on;

(b) cause or procure violence, damage, loss or disadvantage to; or

(c) cause or procure the punishment of,

a person for or on account of the last-mentioned person having appeared, or being about to appear, as a witness at an inquiry by a Commission or for or on account of any evidence given by the last-mentioned person before a Commission.

Penalty: $2,000 or imprisonment for one year, or both.

(2) Without limiting the generality of sub-section (1), an employer shall not—

(a) dismiss an employee from his or her employment, or prejudice an employee in his or her employment, by reason that the employee has appeared as a witness, or has given any evidence, at an inquiry by a Commission; or

(b) dismiss, or threaten to dismiss, an employee from his or her employment or prejudice, or threaten to prejudice, an employee in his or her employment, by reason that the employee proposes to appear as a witness or to give evidence at an inquiry by a Commission.

Penalty:

(a) if the offender is a natural person—$2,000 or imprisonment for one year, or both; or

(b) if the offender is a body corporate—$10,000.

(3) In any proceedings arising out of sub-section (2)—

(a) if it is established that the employee was dismissed from, or prejudiced in, his or her employment and that, before he or she was so dismissed or prejudiced, he or she appeared as a witness, or gave any evidence, at an inquiry by a Commission—the burden lies on the employer of proving that the employee was not dismissed or prejudiced by reason that he or she so appeared as a witness or gave evidence; or

(b) if it is established that the employee was dismissed, or threatened with dismissal, from his or her employment, or was prejudiced, or threatened with prejudice, in his or her employment and that, before he or she was so dismissed, threatened with dismissal, prejudiced or threatened with prejudice, he or she proposed to appear as a witness, or to give evidence, at an inquiry by a Commission—the burden lies on the employer of proving that the employee was not so dismissed, threatened with dismissal, prejudiced or threatened with prejudice by reason that he or she proposed so to appear as a witness or to give evidence.

PART VIII—MISCELLANEOUS

Act not to render other controls illegal

52. Subject to sub-section 35 (2), nothing in this Act shall be taken to render unlawful any release of organisms for the purpose of the biological control of other organisms if the release of the first-mentioned organisms would, but for this Act, be lawful.

Revocation of declarations

53. **(1)** The Authority may, by notice published in the *Gazette*, revoke any declaration made under this Act.

(2) Where—

(a) the Authority revokes a declaration declaring organisms of a kind to be target organisms; and

(b) by reason of that revocation there would be no target organisms for the purpose of controlling which organisms of a kind have been declared to be agent organisms,

the Authority shall revoke the declaration declaring those last-mentioned organisms to be agent organisms.

Declarations continue in operation

54. Where a declaration in relation to agent organisms is in force, those organisms may be released in accordance with section 35 notwithstanding the length of the period of time that has elapsed since the last release of those organisms took place.

Service of documents on Authority

55. Where a person is entitled by this Act to make an application to the Authority or to submit particulars to the Authority, the person shall do so by causing the application or particulars to be lodged at the principal office of the Department in Canberra.

Application for review

56. **(1)** Application may be made to the Administrative Appeals Tribunal for review of—

(a) a decision of the Authority for the purposes of section 19 not to hold an inquiry;

(b) a decision of the Authority for the purposes of section 20, being a decision that is inconsistent with a finding or recommendation of a Commission referred to in Part VII, the Industries Assistance Commission, or a commission referred to in the *Environment Protection (Impact of Proposals) Act 1974*;

(c) a decision of the Authority under section 26 not to publish a notice in any newspaper or journal;

(d) a decision of the Authority for the purposes of section 28 not to hold an inquiry;

(e) a decision of the Authority for the purposes of section 29, being a decision that is inconsistent with a finding or recommendation of a Commission referred to in Part VII, the Industries Assistance Commission, or a commission referred to in the *Environment Protection (Impact of Proposals) Act 1974*;

(f) a decision of the Authority for the purposes of section 30;

(g) a decision of the Authority for the purposes of section 31, being a decision that is inconsistent with a finding or recommendation of a Commission referred to in Part VII, the Industries Assistance Commission, or a commission referred to in the *Environment Protection (Impact of Proposals) Act 1974*;

(h) a decision of the Authority for the purposes of section 33 not to hold an inquiry; or

(j) a decision of the Authority under section 53 to revoke a declaration.

(2) In sub-section (1), "decision" has the same meaning as in the *Administrative Appeals Tribunal Act 1975*.

Regulations

57. The Governor-General may make regulations, not inconsistent with this Act, prescribing all matters—

(a) required or permitted by this Act to be prescribed; or

(b) necessary or convenient to be prescribed for carrying out or giving effect to this Act.

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Echium plantagineum in Australia: Effects of a Major Conflict of Interest

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Abstract

Biological control of *Echium plantagineum* by CSIRO formally began in 1972. Four species were approved for importation and release in Australia: a leaf-mining moth, *Dialectica scalariella*; two flea beetles, *Longitarsus aeneus* and *L. echii*; and a stem-boring beetle, *Phytoecia coerulescens*. Seven other insects (two crown-boring weevils, *Ceutorhynchus geographicus* and *C. larvatus*; two cell-sucking bugs, *Dictyla echii* and *D. nassata*; a bud-feeding moth, *Ethmia bipunctella*; and two flower-feeding beetles, *Meligethes planiusculus* and *M. tristis*) complete the guild likely to be approved for introduction and release. Two pathogens (the powdery mildew, *Erysiphe horridula*, and the fungus, *Cercospora echii*) are also potential agents, but due to current restrictions against importation of these types of pathogens, they are unlikely to be approved. Three limited releases of *D. scalariella* were made in 1980. It showed signs of establishment at one release site, but host plants were eliminated by drought and grasshoppers. An injunction against importation and release of the *Echium* insects, granted on behalf of two apiarists and two graziers in July 1980, followed by a perpetual injunction accepted by CSIRO in June 1983, has prevented further releases or importations. The effects of this injunction and new legislation for biological control in Australia are discussed.

Echium plantagineum: Programme de Lutte Biologique en Australie Interrompu par une Injonction

Le contrôle biologique de *Echium plantagineum* par la CSIRO a officiellement commencé en 1972. L'Australie a approuvé l'introduction de quatre espèces d'insectes au pays: *Dialectica scalariella*, *Longitarsus aeneus* et *L. echii*, et *Phytoecia coerulescens*. Sept autres espèces d'insectes (*Ceutorhynchus geographicus*, *C. larvatus*, *Dictyla echii*, *D. nassata*, *Ethmia bipunctata*, *Meligethes planiusculus* et *M. tristis*) et une maladie (*Erisiphe horridula*) complètent la gamme des agents destinés aux essais de spécificité d'hôte en vue de leur introduction potentielle. *D. scalariella* a fait l'objet de trois essais limités d'introduction en 1980. Un site d'introduction a semblé être favorable à leur établissement, mais les plantes hôtes ont été détruites par la sécheresse et les sauterelles. En 1980, une injonction, faite à la demande de deux apiculteurs et de deux exploitants de pâturage, a mis fin au programme *Echium* et a arrête l'introduction et l'importation d'agents biologiques. Le rapport traite des conséquences de l'injonction sur le programme.

Introduction

Echium plantagineum L. (Boraginaceae), Paterson's curse/salvation Jane, is a major winter-growing, herbaceous annual (occasionally biennial) weed in Australia (Delfosse and Cullen 1981). It is also a weed in Tunisia, Argentina, Morocco, South Africa and Uruguay (Holm *et al.* 1979). There are two other herbaceous, noxious *Echium* spp. in Australia, *E. italicum* L. (Italian bugloss) and *E. vulgare* L. (viper's bugloss), and several woody, ornamental *Echium* spp. (Piggin 1979). The genus originated in Mediterranean climatic areas of Europe and North Africa.

Tillyard (1928) first raised the possibility of biological control of *E. plantagineum* in Australia. Work on this program formally began by the CSIRO Division of Entomology's Biological Control Unit, Montpellier, France, in 1972 (Delfosse and Cullen 1981; Wapshere 1981). Delfosse and Cullen (1981) summarized the work done on this project to 1980, including a brief discussion of the conflict of interest, the most intense of any program in the history of biological weed control. Cullen and Delfosse (1985) expanded the discussion on conflict of interest of *Echium* in Australia, and described legislation (the *Biological Control Act 1984*) (Commonwealth of Australia 1984) which resulted from this conflict.

In this paper I discuss several recent aspects of this program, including the potential biological control agents, the effect of the 1980 injunction on the *Echium* program and biological control in Australia in general, and the likely effects of the legislation in Australia.

Biological Control Agents for *E. plantagineum*

Eleven insect species found in the western Mediterranean appear to have major potential for biological control of *E. plantagineum* (Table 1) (Wapshere 1981, 1983, 1985). Four of these were imported to Australia in 1979–80; one was released in the field. There are also two fungi known to attack *Echium* and other Boraginaceae. Many other species have been recorded on *Echium* spp. in the western Mediterranean (Wapshere 1985), some of which also have potential as biological control agents. The phytophagous guild on *Echium* spp. is discussed briefly below.

Coleoptera

Two univoltine flea beetle species have been approved by the Commonwealth Department of Health, Plant Quarantine, for importation and field release. *Longitarsus aeneus* Kutsch (Chrysomelidae) adults feed on *Echium* foliage, creating 'shot holes'; larvae produce the most damage to plants, and feed on rootlets and the external cortex of the tap root (Wapshere 1981, 1985). *L. echii* Koch adults also produce shot holes in leaves, but larvae feed internally in the main tap root. Adults of both species emerge from soil in autumn. Eggs are laid in winter, and pupation occurs in soil in spring.

Shipments of both species were sent from Portugal and France to Australia from December to March 1980. A rearing procedure was developed (Delfosse, unpubl. data), but it was decided to concentrate on *Phytoecia coerulescens* (Scopoli) (Cerambycidae) and *Dialectica scalariella* (Zeller) (Lepidoptera: Gracillariidae), and no further work was done on the *Longitarsus* spp. in Australia.

P. coerulescens is a univoltine stem-borer of Boraginaceae, especially *Echium* spp. (Kirk and Wapshere 1979). Adults feed on cauline leaves, and larvae feed in the stem in spring, and in the root in summer, thus reducing seeding. It is considered to be a useful member of the guild of biological control agents because it can reduce seeding of the thinner, multi-stemmed *E. plantagineum* found in dense stands; its effect is likely to be less on thick, single-stemmed plants which occur in less-dense stands of the weed (Kirk and Wapshere 1979).

P. coerulescens was received in Canberra from September to November 1979, having been collected originally near Montpellier. It was cleared of its parasites and diseases (Delfosse and Smith, unpubl. data), and was being mass-reared in live plants and artificial diets in preparation for releases in 1980–81. However, the interim injunction granted against the program prevented planned releases (see below) (Delfosse and Cullen 1981).

Table 1. Voltinism, damage and specificity of biological control agents for *Echium plantagineum* L. (Boraginaceae).

Species	Generations per year	*Echium* Stage attacked by			Specificity
		Adults	Nymphs or Larvae	Spores or Mycelia	
Coleoptera					
Cerambycidae					
[1] *Phytoecia coerulescens* (Scopoli)	1	leaves	stem, tap root	_	Boraginaceae
Chrysomelidae					
[1] *Longitarsus aeneus* Kutsch	1	leaves	diffuse roots & cortex of tap root	_	*Echium* spp.
[1] *L. echii* Koch	1	leaves	tap root	_	*Echium* spp.
Curculionidae					
[2] *Ceutorhynchus geographicus* (Goeze)	1-2	leaves, petioles	collar, tap root	_	*Echium* spp.
[2] *C. larvatus* Schultze	1-2	leaves, petioles	collar, tap root	_	*Echium* spp.
Nitidulidae					
[3] *Meligethes planiusculus* Heer.	unknown	flowers	flowers	_	probably Boraginaceae
[3] *M. tristis* Sturm.	unknown	flowers	flowers	_	probably Boraginaceae
Hemiptera					
Tingidae					
[2] *Dictyla echii* Schr.	2-3	shoot	shoot	_	Boraginaceae
[2] *D. nassata* Puton	2-3	shoot	shoot	_	Boraginaceae
Lepidoptera					
Ethmiidae					
[3] *Ethmia bipunctella* Fabr.	3	N.A.[4]	shoot & flower buds	_	probably mainly *Echium*
Gracillariidae					
[1] *Dialectica scalariella* (Zeller)	5-7	N.A.	leaves & stem epidermis	_	Boraginaceae
Fungi					
Moniliales					
[3] *Cercospora echii* Wint.	several	_	_	leaves	probably *Echium* spp.
Erysiphales					
[3] *Erysiphe horridula* (Wallr.) Lev.	several	_	_	leaves	probably *Echium* spp.

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[1] Host-specificity testing completed, and importation to Australia occurred, before injunction granted in July 1980.

[2] Host-specificity testing completed, but importation and release permits not yet requested.

[3] Host-specificity testing not yet begun, but literature surveys and field examinations indicate host range as given.

[4] N.A. = No attack by this stage.

Two weevil species, *Ceutorhynchus geographicus* (Goeze) and *C. larvatus* Schultze (Curculionidae), have been tested for safety as potential biological control agents for *Echium* (Vayssiéres and Wapshere 1983). Adults feed on leaves and petioles; larvae cause the greater damage to the plant by feeding on the collar (mainly *C. larvatus*) and rootstock (mainly *C. geographicus*). Together, they are perhaps the most destructive of the *Echium* guild, and will be considered for introduction should the program proceed.

The last two species of Coleoptera that could be considered initially for introduction are the flower-feeding *Meligethes planiusculus* Heer. and *M. tristis* Sturn. (Nitidulidae). Both species feed on species of Boraginaceae, including *Echium* spp. (Wapshere 1985). Little work has been done on these species, but they will be examined in detail should the program proceed.

Hemiptera

The cell-sucking bugs *Dictyla echii* Schrank and *D. nassata* Puton (Tingidae) attack flowering shoots of *Echium* spp. in late spring to summer (Vayssiéres 1983). Both species spend autumn to spring under *Echium* rosette leaves. There are 2–3 generations/yr in Mediterranean Europe. Both species were found to be restricted to a small group of Boraginaceae in host-specificity testing (Vayssiéres 1983), with complete development occurring on five genera in addition to *Echium*. These species are capable of significantly reducing seeding of *E. plantagineum*.

Lepidoptera

D. scalariella is a small (adult body length *c.* 5 mm), fragile, multivoltine (5–7 generations/yr in Mediterranean Europe) moth whose larvae mine rosette and stem leaves, and the stem epidermis, of *Echium* spp. (Wapshere and Kirk 1977) and five other boraginaceous genera. As no Boraginaceae are of importance to Australian agriculture (other than weeds), importation/release permits were issued.

Seven shipments of *D. scalariella* (collected from Alcacer, Portugal, and Montpellier and Salagou, France) were received in Canberra from March–June 1980. A *Nosema* pathogen was cleared from one population, and an effective mass-rearing technique was developed (Delfosse and Lewis, unpubl. data). Preliminary releases to test overwintering survival and establishment were made at three sites in New South Wales in June and July 1980 (winter), in preparation for mass-releases, to begin in spring. On 10 July 1980, shortly after the third release of *D. scalariella*, a High Court of Australia injunction was granted on behalf of two graziers and two apiarists, which prevented further releases or importations of any *Echium* agents.

Four months post-release, a small population of *D. scalariella* was developing at one release site (Delfosse, unpubl. data). A severe drought began shortly thereafter, however, and a grasshopper plague (primarily *Phaulacridium vittatum* [Sjost.] and *Austroicetes vulgaris* [Sjost.] [Orthoptera: Acrididae]) invaded the area. The combination of drought and grasshoppers eliminated all *Echium* in the area, and prevented establishment of the moth. *D. scalariella* did not become established at the other sites.

Larvae of *Ethmia bipunctella* F. (Ethmiidae) attack the central bud of elongating *Echium* in spring, thus stopping growth (Wapshere 1985). Larvae of second and third generation moths attack developing flower buds in summer. This is the least common of the frequently-found species attacking *Echium* in Europe, and has more often been collected from the biennial plant *E. vulgare* (Sattler 1967), which is also a weed in

Australia (Delfosse and Cullen 1981). Host-specificity testing for *E. bipunctella* has not been conducted, but it is likely to be confined to mainly *Echium* spp. (A.J. Wapshere, pers. comm., 1984).

Fungi

In late winter, large *Echium* rosettes are attacked by the powdery mildew, *Erysiphe horridula* (Wallr.) Lev. (Erysiphales). The fungus can defoliate rosettes (Wapshere 1985). It attacks a large number of Boraginaceae, and would be a useful addition to the *Echium* guild. However, host-specificity testing has not been conducted on this species, because powdery mildews are presently not approved for importation into Australia as biological control agents by the Department of Primary Industry.

One other fungal species, *Cercospora echii* Wint. (Hyphomycetes), appears to have potential as a biological control agent for *Echium* spp. Its host range has also not been investigated for the same reason as given for *E. horridula*.

Effects of the 1980 High Court of Australia Injunction

Legal aspects of the injunction are discussed by Cullen and Delfosse (1985). The most obvious effect of the injunction on the *Echium* program was the prohibition of further releases or importations of the agents. Initially, this was very disruptive because mass-rearing of *D. scalariella* for releases scheduled to be made in spring 1980 had to be halted. Virtually overnight the change from a mass-rearing procedure to a low maintenance procedure had to be made: several thousand carefully reared *D. scalariella* had to be killed, and only a small colony retained. The injunction was less disruptive at this point to the *P. coerulescens* rearing, because many fewer individuals were being handled at that time during the development of a mass-rearing scheme.

However, a small number of *D. scalariella* were found on *E. plantagineum* plants at the CSIRO Division of Entomology site in March 1982. The plaintiffs were immediately informed, and demanded destruction of all remaining moths in quarantine. This disrupted all experiments then in progress. In an effort to retain the populations for possible future use, several hundred larvae and pupae of each of the three demes from the three original sources in Europe were sent back to Montpellier; the rest of the colony was destroyed in March 1982. Unfortunately, all three shipments were temporarily lost en route to Montpellier. By the time they arrived in Montpellier, adults had emerged and died in the shipment containers.

The plaintiffs also demanded destruction of all living *P. coerulescens*, despite assurances that all adults would be killed as soon as they emerged (in sealed test tubes). The colony was destroyed on 17 December 1982, just when three-year experiments on developing a mass-rearing procedure in artificial diet were reaching a satisfactory result. A perpetual injunction on the *Echium* program was accepted by CSIRO in June 1983 (Cullen and Delfosse 1985). If the inquiry into its biological control (see below) finds that the program would be in the national benefit, CSIRO can apply to the court for lifting of this injunction.

There were wider effects of the injunction than those described for *D. scalariella* and *P. coerulescens*. Biological control reserachers all over Australia became concerned that programs involving weeds with even a small degree of conflict of interest could have been halted by any individual with the smallest interest (in the legal sense) in the weeds' present status. This was probably an over-reaction, as legal standing would have to be established in each case before a court would grant an injunction; i.e., the value of the weed to the plaintiff and any possible loss caused by its control would have to be clearly delineated. However, as conflict of interest could arise with many of Australia's major weeds, and in the absence of legislation protecting approved programs, it was considered a possibility that only those weeds with little or no associated conflict of interest would be investigated in the future.

Fortunately, CSIRO, while being concerned about the disruption of the *Echium* program and possible effects on other programs (both current and potential), continued to be supportive of biological control. There was some feeling that, in a time of diminishing resources for scientific research, resources should not be committed to programs which may be prevented from attaining fruition. However, since the *Echium* legal action began, several new biological control of weeds projects have begun, and a new overseas Unit has been established.

Likely Effects of the *Biological Control Act 1984*

Provisions of this *Act* are discussed in detail by Cullen and Delfosse (1985). With the passage of the *Act*, public benefit became a viable justification for biological control activities in Australia. The *Act* contains provisions for establishment of a *Biological Control Authority* (a Federal Minister, or a State Minister in a state that passes complementary legislation), procedures for obtaining declaration of *target organisms* (pests) and *agent organisms* (biological control agents), procedures for conducting public inquiries for both pests and agents, emergency declaration of pests and agents, appeals, compensation for persons adversely affected by biological control programs, and other matters.

The *Act* covers all biological control programs in Australia, not just those for weeds. There is no statutory requirement to obtain declaration of pests or agents under the *Act*, but if utilized, it provides protection for groups intending to conduct biological control of pests for which there is a likelihood of conflict of interest.

An inquiry will be held for *Echium* and its agents from late 1984–mid-1985. Whatever the outcome of the *Echium* inquiry, the result will set a precedent for biological control in Australia.

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Conflicts of Interest Over Beneficial and Undesirable Aspects of Mesquite (*Prosopis* spp.) in the United States as Related to Biological Control

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Abstract

Honey mesquite (*Prosopis glandulosa*) and velvet mesquite (*P. velutina*) have increased greatly in density within their native ranges in southwestern North America since grazing livestock were introduced. They now infest 38 million ha in the U.S. and an additional large amount in Mexico. Herbicidal controls often are marginally economical in rangelands where production/unit area is low and are marginally effective as well. Biological control is well suited to these conditions.

Direct losses caused by mesquite to the livestock industry in the United States are estimated at $200–500 million annually, plus an additional unknown amount in Mexico; total economic losses including livestock support industries are probably three times this amount. Mesquite causes losses primarily by competing with grasses for limited soil water. In the more arid regions (Arizona, New Mexico, Trans-Pecos Texas), it consistently reduces grass production by 50–90%. The reduced grass cover then allows wind and water erosion and the formation of sand dunes. In areas of higher rainfall (central Texas), controlling mesquite usually doubles grass production for 1–3 yrs but production then decreases to pre-treatment levels; losses are greatest during drought years. Total direct losses are probably 20–30 times the present beneficial values of mesquite. Mesquite also increases the cost of handling livestock on ranches, reduces soil water available for other uses, the pollen cuases allergenic reactions in humans, and its great increase in density has shifted the balance of native plant communities from former grasslands to shrubs.

Mesquite is grown as a shade tree primarily in an area of central Texas where its one-time value is estimated at $100 million, or $7 million/yr for the 14 yrs needed to grow a replacement tree. Mesquite wood has been proposed as a fuel to produce electricity or transportation fuels and high-biomass producing varieties are under development. Commercial energy production may be limited by low rainfall to areas where ground water is available and the cost of mesquite may not be competitive with coal or lignite. Use of the wood for other products is of minor importance and usually cannot compete with other cheaper products, although barbecue wood is presently profitable. Many chemicals have been isolated from mesquite but few uses have been found for any of them. Pods are high in sugars and relished by livestock but erratic yields, high cost of harvesting and processing, and digestive problems if too much is fed limit their usefulness for livestock feed; varieties with higher yield of pods are under development. Pods have little potential for human food but the flowers are a good nectar source and produce fine-quality honey worth *c.* $112,000 to $400,000/yr in Texas.

Few species of native birds and mammals use mesquite substantially. Jackrabbits, the white-throated wood rat, the pocket mouse, and to a lesser extent kangaroo rats, might be reduced in population if mesquite were controlled; however, they are at abnormally high populations now, and contribute to rangeland deterioration. Also, populations of the Gambel quail might be reduced but probably not seriously. Young mesquite plants recently have been shown to fix nitrogen symbiotically in root nodules in a greenhouse, but nodules have seldom been found in nature. Mesquite probably fixes nitrogen in the field in some areas when it grows as a phreatophyte, but fixation in arid upland sites may not occur or may be infrequent. The importance of mesquite wood and pods in subsistence cultures, particularly in Mexico, requires more study; other trees, such as huisache and paloverde, might substitute for some uses. Mesquite control also would improve livestock production of subsistence farmers.

A substantial reduction in density of mesquite by biological control would have a beneficial overall effect on the livestock industry. Adverse effects on the ecosystem would be slight and some beneficial ecological

effects might occur. Commercial utilization of mesquite, most of which is of minor importance, and utilization in subsistence cultures might be harmed, the amount depending on type of natural enemy used. Several very promising natural enemies have been found on mesquite in Argentina; these could be introduced into North America for biological control if conflicts of interest between beneficial and harmful aspects of mesquite can be resolved.

Divergences d'Opinions sur les Aspects Bénéfiques et Indésirables du Prosope (*Prosopis* spp.) aux États-Unis eu Égard à la Lutte Biologique

Le prosope glanduleux (*Prosopis glandulosa*) et le prosope velouté (*P. velutina*) se sont considérablement multipliés dans leurs aires de distribution naturelles du sud-ouest de l'Amérique du Nord depuis l'introduction de bétail au pâturage. Ils infestent maintenant 38 millions d'hectares aux États-Unis et une grande superficie supplémentaire au Mexique. En plus d'avoir une efficacité douteuse, l'utilisation d'herbicides est souvent peu économique en parcours où la production par unité de surface est plutôt faible. La lutte biologique s'avère donc le remède par excellence.

Les pertes directes causées par le prosope au secteur des productions animales américain sont évaluées aux environs de 200 à 500 millions de dollars par année, sans compter les pertes supplémentaires au Mexique dont le montant reste inconnu; les pertes économiques totales incluant les secteurs du soutien de l'élevage sont probablement trois fois plus élevées. Le prosope cause des pertes en pompant le peu d'eau du sol dont auraient besoin les graminées. Dans les régions plus arides (Arizona, Nouveau-Mexique, Transpecos Texas), le prosope réduit régulièrement de 50 à 90% la production herbagère. La couverture herbagère ainsi réduite permet l'érosion éolienne et hydrique, ainsi que la formation de dunes de sable. Dans les régions plus pluvieuses (centre du Texas), la lutte contre le prosope permet habituellement de doubler la production herbagère pendant 1 ou 3 ans, après quoi la production revient aux niveaux de prétraitement; les pertes sont les plus lourdes au cours des années de sécheresse. Les pertes totales directes dépassent probablement de 20 à 30 fois les avantages actuels que le prosope représente. La présence du prosope relève également le coût de manutention du bétail dans les fermes d'élevage, réduit la disponibilité de l'eau du sol pour d'autres usages, son pollen provoque des réactions allergiques chez l'homme et sa multiplication a déplacé l'équilibre des communautés végétales indigènes des prairies herbagères vers les prairies arbustives.

Le prosope est cultivé comme arbre d'ombrage essentiellement dans une région du centre Texas où sa valeur ponctuelle est évaluée à 100 millions de dollars, ou 7 millions de dollars par année pendant les 14 ans qu'il faut pour faire pousser un arbre de remplacement. Le bois du prosope a été proposé comme combustible pour produire de l'électricité ou des carburants de transport de sorte que des variétés à forte production de biomasse sont actuellement mises au point. La production commerciale d'énergie peut être limitée, à caude d'une faible pluviosité, aux régions où l'eau souterraine est disponible et où le coût de production du prosope ne fait pas concurrence au charbon ou à la lignite. L'utilisation du bois pour d'autres produits ne revêt qu'une importance secondaire et ne peut gnéralement pas concurrencer d'autres produits meilleur marché, encore que l'utilisation du bois à barbecue soit actuellement rentable. De nombreux produits chimiques ont été isolés du prosope, mais on leur a trouvé peu d'utilisation. Les gousses sont riches en sucre et sont recherchées par le bétail, mais les rendements irréguliers, le coût élevé de la récolte et de la transformation et certains problèmes digestifs en cas de proportion trop élevée dans la ration limitent leur utilité pour l'alimentation du bétail; on cherce actuellement à créer des variétés plus productives. Les gousses s'avèrent peu intéressantes pour l'alimentation humaine, mais les fleurs sont une bonne source de nectar et produisent un miel de haute qualité d'une valeur d'environ 112 000 $ à 400 000 $ par année au Texas.

Seules quelques espèces d'oiseaux et de mammifères indigènes consomment du prosope en quantité tant soit peu substantielle. La lutte contre le prosope pourrait entraîner une baisse des populations de lièvres, du rat à gorge blance, de la souris à bajoues et, dans une moindre mesure, des rats kangourous; les populations de ces espèces sont toutefois anormalement élevées à l'heure actuelle et contribuent à la détérioration des parcours. Les populations du colin de Gambel pourraient être également touchées, mais sans conséquences graves. La culture de jeunes plants de prosope en serre a récemment révélé qu'ils pouvaient fixer symbiotiquement l'azote grâce à des nodosités des racines, mais ces nodosités se rencontrent rarement dans la nature. Le prosope fixe probablement l'azote en plein champ dans certaines régions où il pousse comme un phréatophyte, mais cette fixation en milieu plus aride des hautes terres peut être rare ou complètement absente. L'importance du bois et des gousses du prosope dans les cultures de subsistance, particulièrement au Mexique, nécessite une étude approfondie; d'autres arbres, comme l'acacia odorant et le paloverde pourraient le remplacer pour certains utilisations. La lutte contre le prosope serait également de nature à améliorer les productions animales des agriculteurs de subsistance.

Une réduction substantielle de la densité du prosope par des moyens de lutte biologique aurait un effet généralement bénéfique sur le secteur de l'élevage. Ces effets nuisibles sur l'écosystème seraient légers et certains

effets écologiques utiles pourraient en découler. L'utilisation commerciale du prosope dont la majeure partie est d'une importance secondaire et son utilisation dans les cultures de subsistance pourraient être touchées, selon le type d'ennemi naturel employé. Plusieurs ennemis naturels très prometteurs ont été découverts sur le prosope en Argentine et pourraient être introduits en Amérique du Nord à des fins de lutte biologique si l'on parvient à résoudre les divergences d'opinions sur les aspects bénéfiques et nuisibles du prosope.

Introduction

The mission of the USDA research unit at Temple, Texas, is biological control of weeds in rangelands of southwestern North America. We believe the only viable approach to biological control is by introducing exotic natural enemies. The other alternative, that of augmenting effectiveness of control organisms already present, appears to be too expensive in rangeland agro-ecosystems where 8–28 ha are required to maintain one animal unit. Most weeds of major importance on these ranges are native. Therefore, if exotic natural enemies are to be found that are sufficiently host-specific to introduce, we must select target weeds that have disjunct natural distributions, with one center in our area and one center in another area of the world or, at least, that have species of the same genus that are native in other areas of the world. Several of our major range weeds are closely related to species native in semi-arid areas of southern South America, particularly in the 'Monte' and the 'Chaco' areas of western Argentina and Paraguay (DeLoach 1978).

We have chosen some native weeds, snakeweeds (*Gutierrezia* spp.; Compositae), *Baccharis* spp. (Compositae), creosotebush (*Larrea* sp.; Zygophyllaceae), mesquite (*Prosopis* spp.; Leguminosae), bitterweed (*Hymenoxys* spp.; Compositae), and the introduced weed, salt cedar (*Tamarix* spp.; Tamaricaceae), as top priority candidates for biological control. Native weeds of lower priority are whitebrush (*Aloysia* sp.; Verbenaceae) and tarbush (*Flourensia* sp.; Compositae) (DeLoach 1981). Promising insects have been found in southern South America for all except salt cedar, and for salt cedar in southwestern Asia.

Mesquite is one of the most damaging weeds of southwestern rangelands for which biological control seems applicable. Mechanical and hand control of mesquite has become far too expensive in recent years for most ranchers to use except in small areas. Chemical control has been only marginally effective (Herbel *et al.* 1974; Bovey and Meyer 1981) and is only marginally economical as well (Whitson and Scifres 1979). In addition, some concern exists about environmental pollution and the most cost-effective herbicide, 2,4,5-T ([2,4,5-trichlorophenoxy]acetic acid), has recently been withdrawn from the market. However, a new herbicide, triclopyr, is about as effective as 2,4,5-T and clopyralid promises to be much more effective than 2,4,5-T (Jacoby *et al.* 1981; Bovey and Meyer, *in press*) but the cost will be greater. A need, therefore, exists for an alternative form of control that is effective, economical, and non-polluting.

Prosopis is a genus of 44 species of usually thorny shrubs or trees of the family Leguminosae (Burkart 1976). The most primitive species is native to northern Africa, and three species are native to southern Asia from India to Israel. The greatest center of diversity is western Argentina and Paraguay, where 30 species are native, especially in the Chaco and Monte areas. A few species occur from Chile to Equador and Columbia (Burkart 1976). The genus had spread to North America by 36 to 25 million years BP when pollen was abundant in Oligocene deposits as far north as British Columbia (Smeins 1983). Carman and Mabry (1975) proposed that mesquite migrated to North America on at least three separate occasions, based on the chemical and taxonomic similarities of North American species with those of South America. Nine species are native in southwestern North America; however, one of these, *P. reptans*

Bentham var. *cinerescens* (A. Gray) Burkart, may be an introduction from Argentina by the early European settlers (Burkart 1976; Johnston 1962). Two species are aggressive invaders and are major pests in rangelands. These are *P. velutina* Wooten (velvet mesquite) that occurs in Arizona, U.S.A., and Sonora, Mexico, and *P. glandulosa* Torrey (honey mesquite, with three varieties) that occurs from eastern Texas and southern Kansas to central Mexico and west to California and Baja California. *P. pubescens* Bentham (screwbean mesquite) is a phreatophyte along western rivers and streams from Texas through southern Nevada to California and to northern Mexico. Five other species, *P. laevigata* (Humboldt & Bonpland ex Willdenow) M.C. Johnston, *P. tamaulipana* Burkart, *P. juliflora* (Swartz) DC., *P. articulata* S. Watson, and *P. palmeri* S. Watson, occur in Mexico and are of unknown importance as weeds. The morphology and anatomy of honey mesquite were studied by Meyer *et al.* (1971), and the phenology, morphology, and physiology were reported by Mooney *et al.* (1977). Bibliographies on or including *Prosopis* have been prepared by Bogusch (1950), Schuster (1969), Smeins and Shaw (1978), Schmutz (1978), and Pedersen and Grainger (1981). Reviews have been edited by Scifres *et al.* (1973), Simpson (1977), and Parker (1982*b*).

A few species of *Prosopis* have been introduced into other areas of the world, notably India, Pakistan, South Africa, Egypt, Kuwait, Australia, Hawaii, and Brazil as beneficial arid land trees for their wood, pods, honey, gum, and erosion control. In several of these countries they have become weedy, at least in some locations, and control measures are needed. Many of these introductions were made when several North American species were all called *P. juliflora*. They are still referred to by this name in these countries, and we cannot be certain from literature the actual species in question.

The main aspects of my research are: (1) to find insects on related plants in other countries that are effective and sufficiently host-specific to release in the U.S.; (2) to resolve conflicts of interest in the U.S. and Mexico arising from the beneficial values of the target weed either for man's uses or in the ecosystem; and (3) to test and release appropriate control organisms in the field. Insects found on mesquite have been reported by Cordo and DeLoach (*in press*) and conflicts of interest are discussed here.

A plant that causes damage in one situation (e.g. on rangelands used for livestock production) may provide benefits in other situations (e.g. when used as an ornamental shade tree or for wildlife food and cover). Conflicts of interest between groups who regard plants differently has long been a concern of biological control workers (Huffaker 1959; DeLoach 1978; Andres 1981) and has now stalled projects that promise control of several serious native and introduced weeds (Andres 1981; Delfosse and Cullen 1981; Delfosse 1985; Cullen and Delfosse 1985). Concern centers not only around the direct values of the target weed, but also around impact of introduced control agents that may feed to a limited extent on closely related non-target native plants, particularly those that may be rare or endangered (Turner 1985; Pemberton 1985).

Of particular concern is whether the control of a native species, especially of widespread dominant species such as *Prosopis* or *Larrea*, or an associated impact on non-target native species, will trigger some unknown and unwanted reaction in the ecosystem that may be of serious consequence (Andres 1981).

Mesquite is probably the most damaging weed in southwestern North America but it also has probably the greatest and most varied types of beneficial values of any weed we would consider for biological control.

Mesquite Invasion of Grasslands

Current distribution and abundance of woody plants in southwestern North America is the culmination of ancient geologic, climatic, and biotic events. Mesophytic tropical forests of the warm, moist climate of the Mesozoic Era gave way to large areas of savannah, grassland, and desert as the climate became more arid during the mid-Tertiary Period, *c.* 25 million yrs BP, and the contest between herbaceous and woody species began. This contest continued through the glacial ages of the Pleistocene Epoch (the last 2 million yrs) and culminated in the last 15,000 yrs with retreat of the Wisconsin glacier and continuation of a general drying trend, followed by extinction of many species of large and small mammals, and finally increase in human populations (Smeins 1983).

During the last 100 yrs, the most remarkable phenomenon in the vegetational history of arid and semi-arid southwestern North America has been the extent to which pre-existing plant communities have suffered large-scale invasion of former grasslands by both native and alien species. The chief invaders have been woody species such as mesquite (Harris 1966).

Records of the earliest travelers and settlers indicate that mesquite has not substantially increased its geographical range, but it has greatly increased in density within that range (Bogusch 1951, 1952). In southern Texas, some areas originally were grassy plains but most areas also supported some brush and some areas were in dense stands of mixed species of brush; the major change was from mesquite prairie to mesquite brush (Inglis 1962; Johnston 1963). In the mid-1850s, much of the Texas High Plains, Rolling Plains, and Edwards Plateau was covered by large expanses of unbroken grassland with no trees or shrubs, but in other areas mesquite grew in valleys and in scattered groves along swales or rocky knolls; some travelers described some of the area as covered with groves of mesquite (Box 1967). Today in the United States, 38 million ha are infested with mesquite (Platt 1959). In Texas, 64% of the 34.7 million ha of native rangelands is infested with mesquite, 61% of it with moderate or dense stands (> 10% canopy cover). The areas of rangelands infested by mesquite in the major land resource areas of the State is 85% in the Rolling Plains, Rio Grande Plains, and Blackland Prairie, 55–62% in the Edwards Plateau and Trans-Pecos, 43–45% in the High Plains and North Central Prairies, 97% in the Central Basin, 28–33% in the Texas claypan and Grand Prairies, and minor amounts in other areas (Smith and Reichenthin 1964; Whitson and Scifres 1979).

In the more arid western regions, some areas were characterized by extensive grassy plains in the mid-1800s, some had grass-mesquite savannahs, and a few areas had dense stands of mesquite. Several places mentioned by early travelers that can be identified today demonstrate that mesquite has increased greatly in density and abundance (Humphrey 1958). York and Dick-Peddie (1969) concluded that in the mid-1800s the mesas in New Mexico were grass covered, with mesquite occurring in limited areas on sandy soil or around old Indian campsites. A re-examination of the areas described in the original survey records revealed a great increase in mesquite, creosotebush, juniper, and other shrubs. Buffington and Herbel (1965) reported that mesquite occupied 26.3% of the Jornada Experimental Range in the original survey of 1858 and had increased to 69.6% of the area in 1963. The area dominated by pure stands of dense mesquite had increased 10-fold during that period, from 2537 to 26,782 ha. A similar invasion was documented at the Santa Rita Experimental Range in Southern Arizona. In 1904, more than half the range was classed as grass-dominated, but by 1954 this had decreased to < 20% of the total area. Mesquite covered almost the entire range in some degree, 79% of it in dense and moderate stands (Humphrey and Mehrhoff 1958). York and Dick-Peddie (1969) stated that most of the soil horizon in southern New Mexico that supported grass 100 yrs ago has washed away or formed into dunes. They added that this area can now be considered a 'desert climax' rather than the 'desert grassland climax' as it was previously designated.

The rapid invasion of grasslands by mesquite has occurred since the introduction of grazing domestic livestock by western man. The reasons usually given are: (1) overgrazing and fencing; (2) spread of seed by livestock; (3) suppression of range fires; (4) reduced competition from grasses; and (5) periodic droughts (Buffington and Herbel 1965). The effects of these factors were increased by fencing and digging wells pumped by windmills (allowing cattle to graze in areas far from streams) and came to a sudden climax in the cattle boom of the 1880s when the number of cattle on southwestern ranges increased 6–18-fold above previous levels (Fisher 1977). However, rangeland management that is sufficiently exact to prevent mesquite invasion is very difficult because the strategy of survival of mesquite is so intimately adapted to coexistence with livestock.

As discussed in more detail later in this paper, mesquite foliage is unpalatable and little damaged by cattle, thorns give added protection to young plants and foliage of older plants, but thorns offer little protection to seed pods. Pods are sweet, indehiscent, and are greatly relished by cattle. Seed are not harmed when eaten, and germination is improved and seed-feeding insects are killed by digestive processes. Dung in which seed are deposited on ground provides water and nutrients that greatly favor seedling establishment. Grazing reduces competition from grass which also favors seedling establishment. Grazing also reduces incidence and severity of fires, to which small mesquite plants are susceptible, by reducing the fuel available to burn. Competition from grasses is further reduced by droughts because grasses are more susceptible to drought than the deeper-rooted mesquite plants; also, grasses are more severely damaged by grazing during droughts. Janzen (1969) proposed that seed dispersal is of great importance for mesquite seed to escape from the almost certain destruction by bruchid beetles if they remain under the tree where they fall. Solbrig and Cantino (1975) provided evidence to support this theory and also pointed out that the great longevity of the seed, rapid taproot growth, and phreatophytic habit were important to survival of mesquite in its semi-arid habitat. Presence of numerous underground buds on the upper 30 cm of the taproot allows the plant to resprout rapidly if the upper portion is damaged by mechanical or herbicidal treatments or fire (Fisher 1977).

The mesquite–cattle relationship may be an anachronism as described by Janzen and Martin (1982) for several large-seeded Central American trees (including *Prosopis*) and their seed dispersal agents, which probably were several species of large, extinct, herbivores. Mesquite's strategy of survival (spread of seed by large grazing herbivores) is not well-adapted to living, native herbivores. Bogusch (1952) stated that as long as grasslands were grazed only by deer, antelope, and moving herds of bison, there was little evidence of invasion by woody members of arroyo floras. He further stated that migratory habits of bison took them north of the range of mesquite months before the first mesquite beans matured, although other workers believe that at least some bison had home ranges of only *c.* 50–80 km. Mesquite also is not well-adapted to the living, native herbivores in its center of development in Argentina, where only llamas and their relatives survive today. However, fossil records indicate that many species of large herbivores were present in both North America and southern South America until the end of the Pleistocene about 10,000 yrs ago (Martin 1963). *Prosopis* probably developed its strategy of seed dispersal and survival as it evolved with these herbivores, a situation it was not able to exploit again for 10,000 yrs until western man introduced cattle and horses.

Since major causes of mesquite invasion are disruptions of the ecosystem by man, one might suppose that proper management would provide control or at least halt continued invasion of shrubs. However, several long-term tests have shown that exclusion of grazing alone is not effective. Addition of other stress factors, particularly fire and phytophagous insects used in a biological control program, would appear to be important to counterbalance the effects of cattle.

The best long-term experiments on grazing exclusion have been conducted on the Santa Rita Experimental Range *c.* 35 km south of Tucson, Arizona, and at the Jornada Experimental Range *c.* 40 km northeast of Las Cruces, New Mexico; some of these grazing exclosures were established in 1915 or earlier and are still maintained.

Brown (1950) studied mesquite increase at Santa Rita in exclosures that provided different degrees of protection from grazing for 18 yrs. Mesquite density increased by 55% with open grazing, but still increased by 24% when cattle were excluded, and by 30% when cattle, rabbits, and rodents were excluded. He concluded that grazing management alone would not prevent mesquite increase. Cable and Martin (1973) found that mesquite stands increased 56% over a 21-yr period even in good stands of grass.

Glendening (1952) and Parker and Martin (1952) reported a similar experiment at the same location, with similar results. They noted that perennial grasses decreased by 95% when mesquite increased. They concluded that: (1) mesquite, once seed trees are present, may rapidly increase in abundance regardless of grazing treatment, and perennial grasses will decrease and sometimes disappear; (2) it is improbable that moderation in livestock grazing will prevent loss of grass in mesquite stands; and (3) on many similarly deteriorated semidesert grasslands now occupied by mesquite, artificial control of mesquite may be the only practical means of rehabilitating desirable grass cover.

Smith and Schmutz (1975) and Schmutz and Smith (1976) found that over a 28-yr period velvet mesquite, *c.* 40 km north of Tucson, Arizona, increased rapidly on both protected and closely grazed ranges. They also concluded that protection from grazing alone does not control mesquite and some other factor such as fire was needed to control it under pristine conditions.

In an area 40 km north of Las Cruces in southern New Mexico, Wright (1982) found that mesquite shrubs on long-established plots continued to increase in numbers and cover in spite of protection from grazing; the few temporary decreases noted were attributed to drought and herbicides.

Meyer and Bovey (1982), near Bryan in eastern Texas, sowed mesquite seed at the rate of 75,000 seed/ha into a good stand of mixed grass that was ungrazed for 8 yrs before and for 5 yrs after seeding; total grasses and forbs averaged 2378 kg dry weight/ha. After 5 yrs, an average of 22 mesquite plants (276 plants/ha) were present in untreated plots and up to 74 plants (927 plants/ha) in plots that were mowed. They concluded that it did not seem possible to exclude establishment of honey mesquite only by competition with grass in native pastures containing viable mesquite seed.

All of these grazing exclusion experiments were protected from fire; occasional burning, as occurs under natural conditions, might have decreased the mesquite abundance. Bray (1904), Cook (1908), Humphrey (1958), and Komarek (1972) after extensive observations and literature review, concluded that until the area was settled by western ranchers, fires were widespread and frequent, and that elimination of range fires was one of the major causes of brush invasion of former grasslands in Texas; grass thrived under burning but seedlings of trees were killed. Small mesquites with trunk diameters < 1 cm are susceptible to being killed by fire but larger trees are increasingly fire-resistant (Glendening and Paulsen 1955; Wright *et al.* 1976). Fire is less frequent in more arid areas, especially areas of < 300 mm annual rainfall, because less grass is available to carry the fire. The Jornada Experimental Range has no recorded history of fire in over 100 yrs (Buffington and Herbel 1965) but fire has occurred frequently in northern Arizona (Weaver 1951) and southern Arizona (Humphrey 1963). In arid areas, slow growth of young mesquite trees holds them in the susceptible size range for many years, thus increasing chances that they might be burned. Many workers have proposed that fire is one of the most, if not the most, important factor in maintaining native grasslands free of shrub invasion, not only in the United States but in other grassland areas of the world as well (Komarek 1972; Vogl 1974; Scifres 1980; Wright and Bailey 1982).

Undesirable Aspects of Mesquite

Loss of Grass

Competition by mesquite roots for limited soil water causes a drastic reduction in growth of beneficial forage grasses for livestock grazing. Losses vary with rainfall of the area, density of mesquite, and other factors. Experiments to measure forage losses on the range have seldom been attempted because they require large plots that can be controlled for many years. However, some long-term (5–20-yr) experiments have demonstrated rather conclusively that substantial and continued increases in grass productivity result from mesquite suppression. The more arid regions of Arizona, New Mexico, and the Trans-Pecos area of Texas appear to suffer the greatest losses. Mesquite can completely replace grasses in 'mesquite sand dune' areas of southern New Mexico.

At the Santa Rita Range in Arizona, where mean annual precipitation ranges from 254–508 mm (10–20 inches) depending on elevation, production of perennial grasses was twice as great in plots where mesquite was controlled (338 kg/ha) as in the mesquite-infested plots (160 kg/ha) where mesquite averaged 314 trees/ha with a 16.5% crown cover; both treatments were grazed year-long by cattle. During three drought years, 89% of the grass died in mesquite-infested plots and only 43% died where mesquite was killed. In the same test, annual grasses produced 5 times as much forage where mesquite was controlled (114 kg/ha) as where it was not controlled (23 kg/ha) (Parker and Martin 1952).

Parker and Martin (1952), in a different experiment at Santa Rita, thinned mesquites to final densities of 62, 40, 22, and 0 trees/ha; the unthinned control averaged 435 trees/ha. All plots were open to grazing by cattle. Herbage production of native grasses over 5 yrs averaged 67 kg/ha in unthinned plots, 118 kg/ha in plots with 62 trees/ha, 237 kg/ha with 40 trees/ha, 280 kg/ha with 22 trees/ha, and 298 kg/ha in plots with no trees remaining. In the 14th year of this experiment (1958), total grass production averaged 168 kg/ha where mesquite was not thinned, 417 kg/ha in plots with 62 trees/ha, and 1032 kg/ha in plots with no mesquite, a 6-fold increase (Martin and Cable 1962).

Also at Santa Rita, Cable (1976) measured the effect of killing mesquite on production of native grasses and Lehmann lovegrass (seeded in 1954) over a 20-yr period from 1954–74. During the first 5 yrs before lovegrass became well-established, native grasses produced 2.3 times more (684 *vs.* 299 kg/ha) and lovegrass produced 3.4 times more (281 *vs.* 83 kg/ha) where mesquite was controlled. During the last 15 yrs, lovegrass competition seriously reduced native grasses; natives produced about the same amount with or without mesquite (*c.* 168 kg/ha) while lovegrass produced 1.7 times more where mesquite was removed (917 *vs.* 535 kg/ha). Cattle stocking rate was 10.2 head/259 ha (section) from 1943–53 before mesquite control, compared to 21 head/section during the study period.

At the Jornada Range in New Mexico where annual precipitation averages 225 mm, Paulsen and Ares (1961) reported that three pastures infested with brush (mostly mesquite) decreased in carrying capacity from *c.* 20 ha/animal unit (AU) in 1916 to 81 ha/AU in 1961. The carrying capacity of three nearby grass pastures not infested with mesquite remained generally at 12–20 ha/AU during this period.

Herbel (1977), also at Jornada, sprayed mesquite sand dunes twice with 2,4,5-T (in 1958 and 1961) and left an adjacent area unsprayed; both areas were grazed continuously by cattle. Yield of perennial grasses averaged 6.2 times more on the plot where mesquite was killed than on the untreated plot (204 *vs.* 33 kg/ha) over a 13-yr period 1963–75. Gibbens (1983), in a different study of the Jornada mesquite dunes, found that perennial grass production was 7-, 8-, and 4-fold greater in a 3634 ha plot during the first 3 yrs where mesquite was killed than in an adjacent plot where mesquite remained untreated; production was about the same the fourth year because the untreated plot received more rainfall. Production of all plants (excluding mesquite) was 3-, 4-, and 2-fold greater during the first 3 yrs where mesquite was killed but was 28% greater in the untreated plot the fourth year. Both plots were grazed continuously by cattle except for the sampling exclosure which was moved each year.

At six locations in southeastern New Mexico, Herbel *et al.* (1983) found that over a 3-yr period 1965–67, yield of perennial grasses increased from 10–240% and averaged 76% more in plots where mesquite was aerially treated with 2,4,5-T (mortality of mesquite trees ranged from 7–50% and averaged 36%); at four locations where 38–50% of the mesquite was killed, grass yield increased by an average 107%. Herbel *et al.* (1983) also reported that over an 11-yr period (1963–73), untreated plots produced only 20% as much perennial grasses as did three adjacent plots where mesquite was treated. They pointed out that grass production could increase only if proper grazing management was practiced, particularly by deferred grazing after treatment so that existing grass plants could improve their vigor and new seedlings could become established.

In areas of Texas east of the Pecos River where annual precipitation is 550–950 mm, most measurements of influence of mesquite on forage production have been of short duration (3–4 yrs) and results have varied considerably, depending on location and rainfall during the study period. In many areas, when rainfall is high or normal, sufficient soil water apparently exists for good growth of both mesquite and grass; strong competition for soil water and reduction in forage production occurs mostly in drought years. Scifres and Polk (1974) stated that losses in forage were not apparent if mesquite canopy cover was < 20%. Scifres *et al.* (1977) documented a 50% increase in grass production the first year and doubled grass production the second and third years after spraying mesquite with 2,4,5-T plus picloram in southern Texas.

Kennedy (1970), in the Rolling Plains of northern Texas, found that herbage yields declined by 12% in low density brush (0–10% canopy cover), by 36% at medium densities (10–20% canopy), and by 85% at high densities (20–100% canopy).

Dahl *et al.* (1978), during 5 yrs (1970–75) at three sites in the Rolling Plains of northwestern Texas, obtained an 84% increase in grass production the first year after spraying mesquite with 2,4,5-T (76% root kill of a stand with 27% canopy cover); the second year the increase was 3%, the third year 26%, and the fourth year 11%. Average increase over the 5 yrs of the study was 22%. They calculated that in order to recover the cost of treatment, an increase of 648 kg of grass/ha was needed, which would require 100% kill of mesquite with a 10% canopy cover, 90% kill of a 20%

cover, 80% kill of a 30% cover, 70% kill of a 40% cover, and 60% kill of a 50% canopy cover. Thus, spraying light stands of mesquite would not be economical and only optimal spraying conditions resulting in a high kill would be economical in dense stands. McDaniel *et al.* (1978), also in the Texas Rolling Plains, obtained an average 22% increase in grass production over a 4-yr period after killing mesquite with a 22–29% canopy cover.

A higher incidence of better forage species, higher forage quality, and more grazing by cattle have been observed under the mesquite canopy than in the openings between trees in Arizona (Tiedemann *et al.* 1971; Tiedemann and Klemmedson 1973, 1977; Barth and Klemmedson 1978) and in Texas (Haas *et al.* 1976; Brock *et al.* 1978). Killing the mesquite tree increased grass production under the canopy and increased it more when artificial shade was added; 3 yrs later, differences between former canopy and open areas had disappeared (Tiedemann *et al.* 1971). Tiedemann and Klemmedson (1973, 1977) speculated that mesquite redistributes nutrients from beyond the canopy to areas underneath the canopy; they found that organic matter, nitrogen, sulfur, and soluble salts were *c.* 3 times greater under the tree than between trees. On the other hand, Virginia and Jarrell (1983) and Felker, Lesney *et al.* (1982), working in California, believe that mesquite trees fix nitrogen. This, then, might contribute to the increase of grass under the trees. The best-documented effect of the mesquite on reducing forage production is its competition for water in areas of limited rainfall, as discussed below.

Loss of Beef

The loss in beef production (in kg/ha) is even more difficult to measure than loss of forage. Large pastures are needed for several years, site differences are great, year-to-year differences are great, climatic zones vary greatly, and balancing stocking rates with forage production in different pastures is not exact. Loss of livestock production is not proportional to loss of grass because stocking rates often are based on forage availability at critical times of the year (winter or dry season) rather than on total annual forage production. However, several attempts have been made to estimate livestock losses by various methods.

Fisher and Meadors (1953), at Spur in northern Texas, reported a 20% increase in steer weights over an 8-yr period in pastures where mesquite had been controlled; during two dry years, gains were 48% greater. Robison *et al.* (1970), also at Spur, reported 4–5% increase in cow weight and a 9% increase in calf weaning weights over 8 yrs in pastures where mesquite was controlled.

Workman *et al.* (1965) calculated that mesquite control allowed an increase in stocking rates of 29% on upland sites and 20% on bottomland sites the second year after aerial spraying with 2,4,5-T; this increase was maintained for 2–3 yrs, then declined by 2–3%/yr until the original stocking rate was reached 10–12 yrs after treatment. These conclusions were based on interviews with ranchers in two counties of the Rolling Plains of northern Texas.

Cross and Fisher (1975) reported results of a 5-yr experiment in three areas of Texas. At Matador (Rolling Plains) weights of weaner calves were 19% greater in pastures where mesquite was controlled, at Monahans (Trans Pecos) calf weights were 16.8% greater, and at Menard (Edwards Plateau) calf weights were 4.7% greater and lamb weights were 6.2% greater than on pastures where mesquite was not controlled.

Extrapolation of livestock losses in experimental pastures to total losses in the entire area infested by mesquite in the U.S. and Mexico is not very accurate because: (1) the losses caused by different densities of mesquite in different rainfall zones is not well known; and (2) the area infested at different densities is not well known. Several additional long-term, expensive experiments in different climatic zones are needed to provide adequate information on the first problem. Hopefully, remote sensing techniques under development by the USDA's Agricultural Research Service at Weslaco, Texas (J.H. Everitt, pers. comm.) and by Cornejo *et al.* (1982), together with extensive surveys of brush and forage plant densities such as recently done by the USDA's Soil Conservation Service in Texas (H.H. Senne, Jr., pers. comm.), will provide information for the second problem.

Loss of Soil Water

The basis for most of the observed association between low forage production and high density of mesquite is undoubtedly that mesquite competes strongly with grasses for available soil water. Mesquite has roots that extend > 15 m beyond the tree canopy. In favorable sites roots extend to 15 m deep (a maximum of 45 m has been recorded) though this depth is not attained on most sites. The literature on use of water by mesquite was recently reviewed by Dahl (1982).

Evapotranspiration rates (Gay and Sammis 1977; Tromble 1977; Wendt *et al.* 1968) and vapor pressure deficits (Nilsen *et al.* 1981) have been measured. Richardson *et al.* (1979) near Temple, Texas, found that killing the mesquite on a watershed reduced evapotranspiration by 8 cm/yr and increased surface runoff by 10%.

Parker and Martin (1952) at Santa Rita in Arizona, found that mesquite severely depleted soil water to a depth of 45 cm and to a distance of 9 m from the tree; the number of water deficit days for grasses was 3–8 times more where mesquite trees were alive than where they were killed. Cable (1977), at the same location, found that large mesquite trees used up all of the fall and winter recharge water to a depth of 3 m and out to 10 m beyond the canopy by the end of the usual May–June drought. Trees first used water at shallower depths nearer the tree and as soil water decreased they used water further out and deeper. Finally, as drought increased, the tree used water in the zone from 10 m to at least 15 m beyond the canopy. Competition with grass in the openings between trees was most severe in dry years. The root zone of a tree this size (4 m canopy radius + 15 m of roots beyond the canopy) occupies 0.028 ha and roots of only 35.3 such trees/ha would occupy all the area if evenly spaced.

Honey mesquite is often mentioned as a problem phreatophyte along southwestern streams, along with salt cedar, willow, and *Baccharis* (Timmons 1962; Busby and Shuster 1971; Tromble 1972; Bouwer 1975; Gay and Sammis 1977). *P. pubescens* is also a problem phreatophyte (Campbell and Dick-Peddie 1964; Hughes 1964). Phreatophytes contribute to flood hazards by blocking stream channels and using excessive amounts of water. Evapotranspiration rates for phreatophytes can be enormous, depending on depth of water table. For example, evapotranspiration by salt cedar in Arizona varied from 122–213 cm/yr in different areas (Shrader 1977). Evapotranspiration in a riparian community of velvet mesquite near Tombstone, Arizona, was 1.07 cm/day during the period of peak water use in the first half of June (Tromble 1972).

Bakke (1915) noted that the largest mesquite trees (up to 0.9 m trunk diam. and 15 m tall) grew in river bottoms while plants growing on upland sites were smaller; he stated that trees could grow large if water tables were not deeper than 12–15 m. Easter and Sosesbee (1975) found that mesquite used water extravagantly when available, as in bottomlands, but used much less on upland, dry sites.

Many anecdotal accounts exist of streams that were dry for many years after mesquite invaded and began flowing again when mesquite and other brush were controlled

(Rechenthin and Smith 1967; Dahl 1982; Moseley 1983) but demonstration of a causal effect in these cases is difficult.

In addition to reducing forage production, mesquite probably reduces considerably the amount of water available for irrigated agriculture and for industrial and urban use. Johnston (1957) calculated that 37.7% of the average annual rainfall of 686 mm in Texas was used by non-economic plants. Rechenthin and Smith (1967) calculated that 10.5 million megaliters (ML) (8.5 million acre-feet) of water could be saved annually with brush control in Texas; since *c.* 36% of all brush in Texas is mesquite, this would equal *c.* 3.7 million ML (3 million acre-feet) that could be saved by mesquite control.

Soil Erosion

Mesquite is generally reported to increase wind and water erosion of the soil when it replaces grasses in the more arid areas of the southwest. Parker and Martin (1952) stated that on sloping, upland sites on the Santa Rita Range mesquite caused sheet and gully erosion by thinning grass cover; on bottomlands, severe gullies drained areas that formerly flooded, reducing the water table and making establishment of grasses more difficult. Cable and Martin (1975) on the same range, found that erosion was reduced where mesquite was killed and grass cover allowed to increase.

Paulsen (1953) found that soil texture was coarser under mesquite trees than under grass, which allowed more infiltration after rains but also allowed more evaporation. Also, organic matter was 16% higher and total nitrogen was 19% higher on the grass site than on the mesquite site. Establishment of mesquite seedlings was better on coarse soil and was markedly reduced by dense grass cover (Glendening and Paulsen 1950).

In southern New Mexico, large areas of former grassland are now in mesquite sand dunes. Mesquite is a strong competitor for the meager soil water, bare areas increase as mesquite grows, and in these sandy areas the unprotected soil is deposited by wind under mesquite plants and eventually forms sand dunes, usually 1–1.5 m high (Wright 1982). Many workers regard these dunes as irrecoverable. Also, one might fear that since mesquite is almost the only plant left, if it were removed, say by biological control, wind erosion would be much worse. However, in plots where mesquite was killed with 2,4,5-T in 1958–61, Herbel *et al.* (1977) found that grass production was 6 times greater than on untreated plots, sand dunes leveled appreciably, and wind erosion was reduced. Gould (1982) reported similar results in a nearby area; 5 yrs after mesquite was killed with 2,4,5-T, vegetation had increased greatly between dunes and amount of blowing soil was 15-fold greater where mesquite remained than where it was killed.

Mesquite has been planted in the deserts of Saudi Arabia, Kuwait, and Pakistan for erosion control and its value for aforestation in these extremely eroded areas is highly acclaimed (Felker 1981; Kaul 1970; Le Houerou 1977). However, in southwestern North America, mesquite appears to be much more a cause of soil erosion by replacing the native grasslands than a cure for erosion.

Management Losses

Several workers have noted that one of the major losses caused by mesquite is the added cost of finding and rounding-up livestock from dense stands for branding, medical treatment, or for sale. Fisher (1975) reported that labor required to gather and handle cattle in northern Texas was reduced by 50% on pastures cleared of mesquite. Workman *et al.* (1965) found, from a survey of ranchers in northern Texas, that total labor/cow was reduced from 10 hrs/yr in brushland to 8.5 hrs/yr where mesquite was controlled, which at today's minimum wages equals $5.02/animal. Dahl *et al.* (1978) speculated that the saving in north Texas after mesquite control might amount to $2.47/ha. The greater losses would occur in areas of higher rainfall where the trees grow larger.

Allergenicity

The first published account of allergy to mesquite pollen was from west Texas in 1927 and since then it has been routinely included in allergy screening of patients in the southwestern U.S. The pollen can be carried long distances by wind: 62% of a group of 100 people were found susceptible to it in Los Angeles, although the nearest tree was over 80 km away (Novey *et al.* 1977). Serious allergenic problems were caused in India (Babu *et al.* 1979) and Kuwait (Ellul-Micallef 1981) by the introduced *P. juliflora*.

Effects on Plant Communities and Animal Populations

The enormous increase in density of mesquite in the last 150 yrs has caused some large disruption of natural plant and animal communities. Mesquite invasion in more arid regions causes the formation of dunes, which allows great increases in population of rodents and rabbits, which in turn act to prevent grass increase and rangeland improvement (Wright 1982). Norris (1950), from previous work of others in southern New Mexico, reported that rodent dens were 7.3 times (82.5 *vs.* 11.4 dens/ha), jackrabbits were 10.7 times (0.46 *vs.* 0.04/ha), and cottontails were 10.5 times (1.14 *vs.* 0.11/ha) more abundant in mesquite sandhills than in nearby black gramma grassland. His tests in mesquite sites demonstrated that production of perennial grasses was increased 4–5 times by excluding rodents and rabbits and 1.5–3.5 times by excluding only rabbits. He concluded that rodents and rabbits exert enough pressure to practically eliminate vegetation improvement.

Wood (1969), at the same location, found a similar situation. Biomass of wood rats and kangaroo rats together was 478 g (4.9 rats)/ha in mesquite dunes and 216 g (2.2 rats)/ha in black gramma, or 2.2 times greater in mesquite than in gramma. Each kangaroo rat ate 2.6 kg and each wood rat ate 7.6 kg of plant material/yr. The banner-tailed kangaroo rat alone destroyed 10% of the area of black gramma by denuding the areas around their mounds. Wood (1969) concluded that the eating, storing, and wasting of food by rodents directly competed with both livestock and big game and impacted sufficiently to prevent poor ranges from improving.

Economic Analyses

Workman *et al.* (1965), based on their rancher survey of stocking rates and costs of production, calculated that mesquite control produced an internal rate of return of 13% on upland and 6.8% on bottomland sites over the 10–12 yr life of the treatment.

In a 28-county area of the Rolling Plains of north-central Texas, incomes of ranchers were estimated to have been reduced by $26.2 million annually by the encroachment of brush, which in that area is mostly mesquite (Kennedy 1970).

Osborn and Witkowski (1974) found that potential rangeland productivity in a 130-county area from south-central to northern Texas was reduced by encroachment of mesquite by the equivalent of 4,681,082 ha of non-infested rangeland. This area was estimated to be capable of supporting 1,374,528 cow-producing units in an average year, with a marketable calf production of 213 million kg (1,045,000 calves at 204 kg each), worth $143.3 million. This reduction was 17.9% of total output of the range livestock sector for Texas in 1967. They also calculated that for each dollar of production by the range livestock sector, $3.16 of additional transactions would be generated to support production requirements. Decrease in total economic activity caused by mesquite in Texas was estimated at $429 million for years with below average herbage production to $832 million for above average herbage production when compared to economic activity in 1967 (= $1.05–$2.04 billion at 1981 prices) (Ethridge *et al.* 1984)).

Ethridge *et al.* (1984), based on the increased grass production from the experiments of Dahl *et al.* (1978), calculated that mesquite control produced a total increased value of beef of $29.85/ha over the 5-yr life of the treatment; gains were $15.12 the first year and decreased by about half for each additional year. The cost of control (aerial spraying with 2,4,5-T) was about $22.00/ha, leaving a net profit of $7.85/ha over the 5-yr period, or $1.57/ha/yr. A similar degree of control (75% top kill) by biological control would cost the rancher nothing and would result in a perpetual return of $19.52/ha ($15.12 plus the $4.40/yr cost of control).

A conservative estimate, by extrapolating from these few available analyses, is that mesquite probably causes direct losses in livestock production of $250–500 million annually in the U.S. and 3 times that amount in total lost economic activity. In addition, large but unknown losses occur in Mexico. However, none of these economic studies calculated the effect that a substantial increase in livestock production (brought about by better control of mesquite) would have on market prices of livestock. Increased production could have disastrous effects in a market already frequently in a depressed state unless offset by lowered cost of production or development of additional markets.

Commercial Utilization of Mesquite

In the 1800s and early 1900s (Palmer 1878; Forbes 1895; Marshall 1947), and again in recent years (Felger 1977; Jatasra and Paroda 1981; Felker 1979, 1981; Haller 1980; Pedersen 1980), mesquite has been portrayed as an all-purpose staple of human culture. It was used in a similar manner in southern South America (D'Antoni and Solbrig 1977). The earlier concept was in relation to its use in Indian cultures and by early western settlers of semi-arid southwestern North America.

Several workers have attempted to extrapolate utilization in the earlier period to utilization in the future, where fossil fuels will have been mostly used up and where arid lands and deserts will have increased. Mesquite may still play a role in present-day subsistence cultures in arid regions where natural resources are scarce and manufactured products too expensive to buy. However, its utilization in industrialized societies is different and many of the supposed potential benefits prove to be economically impractical. Still, great needs will exist in the future, and mesquite may play a role in filling some of them, but the economics of all the alternatives must be examined carefully before concluding that utilization of mesquite is the answer.

Utilization of Wood

Fuel for steam or generation of electricity. Wiley (1977) calculated that a 20% return on the investment could be made by firing a 60,000 pph boiler with naturally occurring mesquite wood. Such a boiler could operate for 10 yrs using the mesquite within a 7.2 km radius and might be suitable for a small industry needing a medium-sized boiler and willing to locate where mesquite is abundant. He concluded that mesquite would not be economical to produce commercial electricity, methane, or methanol.

Felker, Lesney *et al.* (1982), Felker, Clark *et al.* (1982), and Felker (1984) calculated that intensively managed biomass farms, growing high producing *Prosopis* selections, could produce 16 metric tons dry matter/ha/yr. This production would support a

500 megawatt (MW) electric generating plant or a large petrochemical plant on a permanently renewable basis if all the land within a 22 km radius (152,000 ha) were farmed. He calculated an average cost of production (excluding interest on investment) of $1.48/million Btu; this compared with natural gas at $3.00/million Btu, crude oil at $6.00/million Btu, and western coal at $1.48–2.60/million Btu (Felker 1984).

Sugarman and Rudzitis (1982) compared the advantages and disadvantages of burning mesquite and lignite. The main advantages of mesquite are that it is a renewable resource, it burns much cleaner (0.1% sulfur compared with 19% for lignite), and the cost of controlling it as a weed could be saved. One of the main disadvantages, that it grows in very disperse stands, would be largely overcome if the production projections of Felker, Lesney *et al.* (1982) could be achieved. Several recent developments have made the use of mesquite for energy production seem feasible but other difficulties have been encountered that leave practical, large-scale production questionable.

Among the promising developments is recent progress made by Felker and Clark (1980), Felker, Cannell and Clark (1981), Felker, Clark *et al.* (1981), Felker, Lesney *et al.* (1982), Felker, Clark, Cannell, and Osborn (1981), and Felker, Clark, Nash *et al.* (1982) in selection of strains and hybrids of *Prosopis* for high yield of biomass, high pod production, cold tolerance, and salinity tolerance and in propagating and culturing the plants in the field. Felker, Clark, Cannell *et al.* (1982) calculated yields of 16 metric tons/ha/yr for the best South American hybrids that were growing in a field plot at Riverside, California, by extrapolating yield of individual trees to an area basis. Differences in biomass production varied > 100 fold between selections and largest trees exceeded 6 m in height and 17 cm basal diameter by the end of the second season. In a similar study near Brawley in the southern California desert, Felker *et al.* (1983) obtained maximum yields of 14.5 tons/ha/yr from 2-yr-old high-biomass selections of *Prosopis* in field plots. However, these plots received 580 mm irrigation the first year and 750 mm the second year. Maximum yield of naturally growing *Prosopis* trees in the U.S. was measured by Sharifi *et al.* (1982) at 3.6 tons/ha in a phreatophytic situation in southern California; he considered this to be a very high biomass yield for the desert. Wright and Stinson (1970) found that current year's growth of average mesquite in the Texas Rolling Plains was 1.1 tons/ha and regrowth from cut trees was only 0.24 tons/ha.

In Pakistan, Ahmed (1961) reported timber yields (clear bole) of 8000 kg/ha/yr in small plots over a 12–15-yr period in a 250 mm rainfall zone; nine plots had yields above 3000 kg/ha/yr (no mention was made of possible ground water). From these data, Felker (1979) calculated total above-ground biomass yields of 8000 kg/ha/yr. Salinas and Sanchez (1971) reported that yields of pods and leaves of *P. tamarugo* F. Philippi in Chile were 12,000 kg/ha where ground water was available.

Felker, Lesney *et al.* (1982) found strains of *P. chilensis* (Molina) Stuntz emend. Burkart with water use efficiency of 345 kg water/kg dry matter produced, whereas rangeland accessions from west Texas, New Mexico, and Arizona typically had efficiencies in the range of 2300–2600 kg water/kg dry matter. Felker (1979) calculated water use efficiencies of 250 kg water:1 kg dry matter in a *Prosopis*-dominated savannah in Chile that produced 14.5 tons total biomass/ha/yr in a 361 mm rainfall zone. He also calculated an efficiency of 205:1 from the data of Ahmed (1961) in a 246 mm rainfall zone.

A mesquite harvester has been developed that can cut trees up to 17 cm in diameter, cut it into pieces no larger than 2 × 18 cm, and collect it in a large hopper for a cost of $7.46/green ton (Ulich 1982*a*) or $14.77/dry ton (Ulich 1982*b*). Also, research is in progress on methods of asexual propagation and culture in the field at Texas A & I University (Felker, Lesney *et al.* 1982).

Among the problems encountered, the most serious is probably the question of whether sufficient rainfall exists over most of the range of mesquite to allow sufficient production for biomass farming to be economical. Water use efficiencies are difficult to measure and results from laboratory tests may be greatly different from those under field conditions (Dahl 1982). Also, some efficiencies calculated for *Prosopis* in the field contain possible sources of error. For example, field plots at Riverside, California, used for Felker's measurements are surrounded by citrus and agronomic experimental plots that have been irrigated for many years, and the plots were irrigated for many years before mesquite was planted; this may have allowed accumulation of stored water that mesquite roots could reach. Thus, the trees may have used more water than was calculated. Biomass estimates from other areas of the world indicate that the high production needed for commercial energy production may be achievable. However, high production areas of *P. tamarugo* in Chile have a high water table that the trees utilize. The high producing tests in Pakistan (Ahmed 1961) and other areas of the world might also have ground water available since this was not mentioned in the reports.

Production requirements for commercial electrical or petrochemical production are based on projection of 16 tons of dry matter biomass/ha/yr, grown within a 22 km radius of the plant. A lower production/ha would require harvesting and hauling the wood over a larger area which might not be economical. Felker's high biomass-producing hybrids with the highest water use efficiency (345 kg water:1 kg dry matter) would require 552 mm water/yr. If the trees could use 75% of the annual rainfall (a proportion that might not be achievable), then 736 mm annual precipitation would be required. With a more probable water use efficiency of 500:1, then an annual precipitation of 1067 mm would be required if the trees used 75% of the rainfall, or 1231 mm would be required if they could use only 65% of the rainfall. This much annual precipitation is not available anywhere in the U.S., nor in most other areas of the world, where mesquite grows. Production over much of the southwestern U.S. where rainfall is 300 mm or less would be 3.8 ton/ha or less if water use efficiency were 500:1 and 75% of the rainfall were used.

Realistic production measurements have not yet been made in the field in semi-arid southwestern North America where production is proposed, under non-irrigated, non-phreatophytic conditions, and on a scale large enough to exclude the possibility that the plants are using ground water from outside the plot area. Extrapolation of production from individual trees or small plots may be misleading. Insufficient rainfall would appear to limit intensive, high production biomass farming to areas where ground water or irrigation is available. These are also the most productive agricultural areas which would make land rental there much greater than that budgeted by Felker (1984). The requirement for 560–750 mm irrigation/yr (Felker *et al.* 1983) makes the culture of mesquite in semi-arid and arid areas of the world of questionable value.

Other problems exist in scaling up from small plots to commercial biomass farming. The techniques for asexual propagation of the high yield, high water-use efficiency *Prosopis* selections have not been developed on a commercial scale (Felker, Lesney *et al.* 1982). The best genetic selections for high biomass and water use efficiency are not cold tolerant (Felker, Clark, Cannell, and Osborn 1982; Felker, Clark, Nash *et al.* 1982) and could not be grown in most of the range of mesquite in the U.S.

Insects, pathogens, and weeds are serious problems in the present small field plots (Felker 1984) and could become worse problems in large-scale plantings as has been experienced in many monocultures of agricultural crops. However, most of these problems in propagation and culture can probably be solved with further research.

Several economic problems face utilization of mesquite for production of electricity or petrochemicals. Large electrical plants like those currently in use (300–1000 MW) require a large amount of fuel that, in the case of mesquite, would have to be harvested and transported across a large area, making mesquite uncompetitive in price with coal or lignite. Smaller plants (10–50 MW) require probably a 60% greater investment/kw produced. Burning part wood and part coal would still require a large investment for conversion (Parker 1982*a*). However, an increase in fossil fuel prices and a decrease in interest rates could make the production of electricity from mesquite wood economical (Smith 1982).

Smaller steam boilers are more efficiently fired with natural gas, LP gas, or fuel oil; also wood boilers cost 200% more than gas boilers. Use of mesquite for firing steam boilers in oil fields for steam injection recovery of crude oil is possibly a viable approach if the wells are situated among stands of mesquite (Parker 1982*a*).

Transportation fuels (alcohol and gasoline) can be made from mesquite but the most satisfactory process is by gasification. This requires a very large plant to be economical (equivalent in size to use of 25,000 tons of coal/day); this much mesquite cannot be harvested near enough to the plant to be economical (Parker 1982*a*). However, smaller gasification plants have been developed, including a plant in Tennessee to produce acetic anhydride that uses only 900 tons of coal/day (Coover and Hart 1982). Plants of this size and smaller should make utilization of mesquite wood as a raw material much more feasible, at least for production of industrial chemicals if not for energy.

Steam driers for agricultural products or for energy on individual farms and ranches are possible but would require a large investment and are labor-intensive. Automobiles and tractors can be powered by extracting gases from burning wood. This method was widely used in Europe during World War II but it is inconvenient and maintenance costs are increased by 40%. Newer stationary engines have been under development for small-scale power production but they require pelletized wood which adds to the cost (Parker 1982*a*).

Wood products. In earlier years in North America, mesquite wood was used for many purposes on a small scale by Indians, and by early settlers, and is used to a lesser extent today. However, Peter Koch stated in a communication to the Texas Tech Mesquite Utilization Committee in 1975 that any conventional forest products which might be made from Texas mesquite could be produced more economically from cull trees within existing forest products industry. This statement by a recognized authority on utilization of marginal forest resources should be given serious consideration before investing significant amounts of money and time in converting mesquite to conventional forest products such as wood, paper, or chipboard (Parker 1982*a*).

Firewood and charcoal. Mesquite wood is excellent for fireplace use but other readily available trees are larger and straighter and, therefore, more efficient to harvest.

Charcoal can be made from mesquite but the wood is crooked and difficult to load in kilns (Kotok 1955). Also, producers must compete with already established manufacturers who often use wood by-products obtained cheaply (Parker 1982*a*).

Barbecue wood. Nationwide interest has recently developed in using mesquite wood as barbecuing fuel. This market is developing rapidly and a few entrepreneurs are making good profits, as are farmers and ranchers from the sale of the wood. However, this is a specialized market that probably cannot be developed on a large scale (Parker

1982*a*) and will be of unknown duration. The possible production of carcinogens during combustion of the many chemicals present in mesquite wood has not been investigated.

Crafts and furniture. Mesquite wood is hard, has an attractive color and grain, and is good for making furniture but trees large and straight enough to make boards are rare (Wiley 1975). Mesquite is a favorite of craftsmen and hobbyists for making novelties. Craftsmen, producers of barbecue wood, and other affectionados of mesquite have recently formed an organization for exchange of information on the availability and culture of mesquite wood and the manufacture and marketing of mesquite products.

Paper. Experiments in India indicated that writing and printing papers could be made from the wood of *P. spicigera* L. (= *P. cineraria* [L.] Druce); however, the logs were hard to chip, the yield was low, and the paper was of poor strength compared to that of other hardwoods tested (Guha *et al.* 1970). Also, the bark was difficult to remove and the low yields require hauling it long distances to the plant compared with other woods that are plentiful in the U.S. (Parker 1982*a*).

Utilization in Mexico. In Mexico, 92.7% of the usage of mesquite wood was for charcoal and firewood, with minor usage for fenceposts, bark for tanning, lumber, and cross ties (Lorence *et al.* 1970). Commercial use apparently began about 1935 but has declined greatly since the 1950s mainly because of over-exploitation of the trees large enough to use and because of clearing mesquite forests for pastures and crops. Mesquite is still much used domestically in many areas but this use was not measured (Lorence *et al.* 1970). Some logs and lumber are presently being sold to craftsmen in the U.S.

The degree to which biological control of mesquite would affect subsistence farming cultures, especially in Mexico, is very important and remains to be determined. My personal opinion, from limited observations in Mexico, is that in many areas other trees, especially huisache, *Acacia farnesiana* (L.) Willd., are abundant enough to supply firewood and wood for farm implements and household industries.

Livestock Feed

Leaves. Leaves of certain mesquite species are eaten by livestock in other countries. For example, *P. tamarago* is eaten by goats and sheep in Chile (Elgueta and Calderon 1971) and *P. cineraria* (L.) Druce is eaten by goats and sheep in India (Bhandari *et al.* 1979; Bohra 1980; Sharma 1982). However, leaves of the North American mesquites are little eaten by livestock. Sanders *et al.* (1973) reported that leaves of *P. glandulosa* in Texas were browsed only infrequently in spring and summer and Galt *et al.* (1982) found that velvet mesquite leaves comprised only 3–6% of the diets of fistulated steers in New Mexico in spring and early summer, when they are probably most palatable.

Pods. Ripe pods of mesquite are relished by most livestock, probably because of the high sugar content, and are often mentioned as a valuable feed. Pods of *P. glandulosa* contain 25–34% sugar (mostly sucrose), 8–14% protein, 2.5% fat, 3.4–4.8% ash, and 17–22% fiber; pods of *P. velutina* and *P. pubescens* were similar. The sugar is mostly in the pericarp and protein is mostly in seed (Becker 1982; Meyer *et al.* 1982). The protein is high in several essential amino acids, including lysine, but is low in those containing sulfur; the beans are also a good source of Ca, Mg, K, Zn, and Fe (Zolfaghari *et al.* 1982). Seeds are small and hard and most of them pass through cattle undigested. All reports recommend grinding the beans for best utilization by livestock.

In the U.S.A., Garcia (1916) found that ground mesquite beans were 75% as efficient as corn in the diet of hogs but that efficiency dropped to 53% after feeding for 4 wks.

Ground pods of *P. velutina* were a satisfactory substitute for 20% of the corn in chick diets, but 40% of pod meal reduced body weight (Becker 1982). In Mexico, ground beans are fed to cattle, sheep, goats, horses, burros, mules, and pigs, but they usually make up only 20–50% of the rations (Lorence *et al.* 1970). Cruz (1979), also in Mexico, found that replacing 50% of a balanced commercial feed with mesquite beans was satisfactory for feeding rabbits. The collection and sale of beans is an important source of income for subsistence farmers. A family can collect 100 kg/day of beans and 40,000 tons were collected in 1965, worth $1,100,000 (Lorence *et al.* 1970).

In India, ground pods of the introduced North American *P. juliflora*(?) were satisfactory for up to 20% of the diets of calves, 10% for lactating cows (Talpada *et al.* 1981, 1982), and 45% in a maintenance diet for bullocks (Gujarathi *et al.* 1981). In South Africa, Kargaard and van der Merwe (1976) fed mutton Merino sheep only on pods of *P. juliflora*(?) but digestion of fiber decreased if pods comprised > 40% of the diet.

Dollahite and Anthony (1957) and Dollahite (1964) noticed that cattle that ate a lot of pods over an extended period developed an illness characterized by anemia, emaciation, salivation, protruding tongue, and nervousness; autopsies showed that the rumens were filled with mesquite beans. They postulated that the high sugar content of the beans altered the microflora of the rumen so that the animals could no longer digest cellulose or synthesize B vitamins. The importance of this was evident in the reports of feeding trials described above, most of which found that mesquite beans should constitute only a part of the diet.

Pak *et al.* (1977) found low levels of harmful chemicals in seeds of *P. tamarugo* in Chile: 2.3 trypsin inhibited units/mg and 6.0 units of haemagglutins/mg protein. Sharma *et al.* (1979) found high levels of protease inhibitors (640 trypsin inhibiting units/g) in seeds of *P. cineraria* in India. Also, a large number of alkaloids have been found in seeds of *Prosopis* spp., as discussed later, many of which may be toxic. Becker (1982) in Texas found low to moderate amounts of trypsin inhibitors and haemagglutin in seeds of *P. velutina* but these were destroyed by moist cooking. However, the cooked seed gum, although subsequently dried, had an increased water binding capacity and bulking effect that significantly interfered with digestion in both chicks and rats. Ground pods of *P. pubescens* caused a net loss of nitrogen in chicks. In addition, samples of both *P. chilenses* and *P. tamaguro* from Chile contained cyanide (Becker 1982).

Large-scale commercial utilization of mesquite pods is beset with several problems, among them the low and erratic yield of pods of North American mesquites and the difficulty of harvesting and processing them.

Garcia (1916) harvested 17 kg of pods from one (velvet?) mesquite tree in Arizona. Parker and Martin (1952) collected pods from 25 marked velvet mesquite trees for 5 yrs and obtained an average yield of only 0.64 kg/tree/yr and 15.3 kg of pods/ha. They stated that the assumed value of pod production to livestock was greatly overestimated; furthermore, the crop was likely to fail completely in dry years when it was most needed. Goen (1975) observed 25 trees/site in western Texas for 4 yrs and found that only 2% produced as much as 50% of their estimated potential number of pods. Felker (1979) questioned these results, pointing out that most other measurements are about 10 times this great. He harvested 7, 3, 43, and 50.9 kg of oven-dried pods from four trees in California. Cornejo *et al.* (1982) found that 26 mesquite trees at Quartsite and Tucson, Arizona, and Kino Bay, Sonora, produced an average of *c.* 2700 and a maximum of over 8000 pods/tree; pod production was correlated with crown diameter of the tree ($r = 0.823$). My observations near Temple, Texas are that yield varies greatly from tree to tree; scattered trees, or scattered small groups of trees, bear heavily but most trees growing nearby or even adjacent to them have few or no pods. Felker (1979) believed that yield could be dramatically increased by selecting breeding stock with high yield. He found great genetic variation in yield in stock he examined from both North and South America and from various crosses of these but trees from the southwestern U.S. were among the lowest producing. How well these improved strains would compete and survive if cultivated in the harsh climate of this area remains to be seen.

Meyer *et al.* (1982) developed a milling machine that can process 500 kg of pods/hr if they are previously dried to 5% water content. Nonetheless, the cost of harvesting and processing of mesquite beans (except by subsistence farmers or as a by-product of some other use) would probably make them too expensive to compete with cereal grains or soybeans as livestock feed.

Processed wood. Researchers at Texas Tech University have demonstrated the technical feasibility of converting mesquite wood into ruminant feed (Parker 1982*a*; Cox and Tock 1982). However, their economic analyses predict that the product would be competitive in cost with standard livestock feeds (alfalfa hay) only in special situations such as an alfalfa crop failure. Raw mesquite chips cost $9.00/ton delivered to the plant. Treatment with ozone plus catalyst to increase digestibility costs $100.00/ton. The cost, based on equivalent cost and nutritive value of corn, was 20% more than alfalfa hay (Tock 1982).

Human Food

Pods. Aboriginal peoples of southwestern North America ground dry pods into a meal and made bread or soaked pods in water to make drinks or alcoholic beverages. Green pods were boiled with meat or mashed and boiled; seed were ground separately and mixed with pod flour; and the gum was chewed by children (Palmer 1878; Bell and Castetter 1937; Felger and Moser 1971; Brashler 1973; Felger 1977). In other arid zones of the world, native mesquites and the introduced *P. juliflora*(?) are used in much the same way today (Sen and Bansal 1979; Aykroyd and Joyee Daughty 1964; Khasgiwal *et al.* 1969). The value of mesquite for human food in North America is probably insignificant at present. Even among Indian tribes it is probably eaten very little except perhaps on ceremonial occasions. With the continued assimilation of these groups into the cultural mainstream, the use of mesquite for food will probably disappear.

Recent studies at Texas Tech University hold little promise for use of pods in commercial food products. Various fractions of ground pods usually produced a bad flavor, reduced baking quality, and coarseness when added to wheat flour in breads and cookies, although smaller amounts sometimes produced a pleasant or sweet taste (Meyer *et al.* 1982). Some of these unpleasant qualities probably could be corrected by selection of varieties with improved pod quality but mesquite flour would have to compete with other cereal grains and sugars that are plentifully available at a relatively low price.

Honey. Mesquite is one of the more valuable honey plants in the southwestern U.S.; it has two blooming periods, and it produces a good quality, light honey (Sanborn and Scholl 1908; Pellett 1930; E.C. Martin 1979, pers. comm.). Esbenshade (1980) reported that on the island of Molokai, Hawaii, 226,800 kg of honey was produced in 1930, mostly from mesquite. Production/hive averaged 54–68 kg/yr. Total honey production in Texas is roughly estimated at 0.68–1.36 million kg annually. Production from mesquite is variously estimated at 15–30% of the total (Loys Milam, Sioux Pee Co., pers. comm.). This gives a total production from mesquite of 102,000–363,000 kg annually. In some years, nearly all of the honey production over wide areas is from mesquite. At $1.10/kg paid to the beekeepers, the total value of mesquite honey in Texas is $112,000–$400,000 annually. These estimates are based on the best judgments of experts in the field.

A drastic reduction in mesquite in areas of heavy honey production might cause relocation of hives, with some effect on economy of the industry and on location of hives to pollinate other crops. The value of bees for pollination is much greater than for honey. Principal crops pollinated by bees in Texas are cucumbers, cantalopes, watermelons, fruit trees (including citrus), cotton, and sunflowers (Loys Milam, pers. comm.).

Chemicals and Medicines

Identification of chemicals. Mesquite has been widely used as folk medicine by the indigenous peoples of North and South America and Asia from the beginning of history. Many studies have been made to identify the various chemicals in mesquite, especially by Indian, Pakistani, and Argentine scientists, but only a very few minor uses have been reported. Many alkaloids have been identified, for example, by Cercós (1951) and Gianinetto *et al.* (1980) from Argentine mesquites, by Shankaranarayan *et al.* (1979) from the south Asian *P. spicigera*, and by Ahmed *et al.* (1979) from *P. juliflora*(?) introduced into India and Pakistan from North America.

Over 40 flavones have been identified from *Prosopis* spp. by Bhardwaj *et al.* (1979, 1981), Vajpeyi *et al.* (1981), and Shukla *et al.* (1980) from India; Wassel *et al.* (1972) and Shalaby *et al.* (1976) from Egypt; Gianinetto *et al.* (1975) and Gitelli *et al.* (1981) from Argentina; and Bragg *et al.* (1978) from the U.S.A. The flavonoids were also examined for possible taxonomic separation of the various species, as were the amino acids present in many mesquite species (Carman *et al.* 1974).

Gutkind *et al.* (1981) found bacterial and fungal growth inhibitors in extracts of three Argentine mesquites, Ahmed and Agnihotri (1977) found anti-fungal activity in leaf extracts of *P. spicigera* in India, and El-Merzabani *et al.* (1979) found some anti-tumor activity in fruit extracts of *P. juliflora*(?) in Egypt. In Mexico, extracts from the beans of *P. juliflora* reduced transpiration in bean leaves by 15%, with no reduction in yield (Rolim and Gonzáles 1975).

Alcohol. Ethyl alcohol can be made from mesquite wood (Cox and Tock 1982) but it is not economically competitive with ethanol from grain and sugar crops (Tock 1982).

Tannins. Mesquite has often been mentioned as a source of tannin. Tannins were identified from mesquite in Egypt (Shalaby *et al.* 1976; Doat 1978) and from *P. juliflora*(?) in India (Malhorta and Misra 1981). However, Theresa *et al.* (1977) concluded that the tannin content from *P. juliflora* in India (a maximum of 5.2% from heartwood) was too low for industrial recovery. In the U.S., both yield (about 10%) and quality were also low (Parker 1982*a*).

Gums. Gum is produced by mesquite when the cambium layer is injured or when the limbs are cut (Greenwood and Morey 1979; Khasgiwal *et al.* 1969). The gum consists mostly of a highly branched polysaccharide that yields the sugars arabinose and galactose, and methoxy-glucuronic acid in the ratio 4:2:1 (White 1946). The gum is similar to and could be used as a substitute for gum arabic (Khasgiwal *et al.* 1969; Churms *et al.* 1981; Anderson and Farquhar 1982), or gum taraganth (Marshall 1947) and could be used as a source of industrial L-arabinose (Greenwood and Morey 1979). Martinez Ojeda *et al.* (1976) report that 1612 tons of gum arabic are imported into Mexico annually and they believe that Mexican mesquite gum could substitute for this.

A galacto-mannan gum was obtained from the seed (56.5% mannose, 36.2% galactose, 4.2% arabinose, and small amounts of five other monosaccharides) that is very similar to guar gum and has potential for industrial use (Meyer *et al.* 1982). However, collection of mesquite gums would be very labor-intensive and it would have to compete in price with imported gums, those produced from crops that are not labor-intensive (Parker 1982*a*), or with manufactured gums.

Ornamentals

Mesquite is commonly used as an ornamental shade tree in some areas of the southwestern U.S. and Mexico. It is an attractive tree with a light shade and often picturesque form, especially in large trees (Steger and Beck 1973). Species in use are *P. glandulosa*, *P. velutina*, *P. alba*, *P. chilensis*, and at least one hybrid. The decrease in availability of irrigation water makes its use even more attractive since it is very drought resistant (Allworth-Ewalt 1982). *P. alba* selections from Chile are promising as frost tolerant, thornless, evergreen ornamentals (Felker, Lesney *et al.* 1982).

At Temple, we have measured the extent to which honey mesquite is used as an ornamental throughout Texas and adjacent areas of New Mexico and Oklahoma (C.J. DeLoach and T.O. Robbins, unpubl. data). Mesquite trees were counted at more than 10,000 houses in over 100 towns and cities within the range where mesquite occurs. The most intense usage is in a zone through central Texas from north of San Angelo through Eldorado, Mason, and Uvalde to Corpus Christi. Mesquite is less abundant or is absent east of this area and further west the trees are too small to use as ornamentals unless irrigated. In the zone of main usage, mesquites averaged 0.11 small trees/house, 0.54 medium trees/house, and 0.24 large trees/house. Allowing an arbitrary value of $5 each for small trees, $200 for medium trees, and $800 for large trees, this amounts to $300/house within the zone of most common usage. In this zone, 12.7% of all shade trees were mesquite. Use in other zones of the State was much lower. Calculations are still in progress to extrapolate the total number of small, medium, and large trees used in the entire State. It appears that the one-time value of mesquite for ornamentals will approach $100,000,000 in Texas. If this is spread over the *c.* 14 yrs needed to grow a replacement tree, the value would be $7,000,000/yr.

Ecological Values

Wildlife Food and Shelter

Prosopis is an integral part of the desert ecosystem in both North and South America. Many organisms prefer it as food or habitat when it occurs in mixed plant communities. It is a dominant phreatophyte that affects both plants and animals, probably more than most other plants in desert areas. It seems to be more important in the desert ecosystem of the Monte of Argentina than in North America. Plants and animals are associated with it in an obligate manner there, while in North America this tendency is less pronounced (Mares *et al.* 1977). Although mesquite has been present in North America at least 25–36 million years (Smeins 1983), it is of even more ancient origin in South America, and the genus has much more variation there, providing opportunities for more species of animals to adapt to it.

Because of the large area occupied by mesquite and its dominant position in the ecosystem, effects of various degrees of reduction of mesquite on the other members of the ecosystem should be considered (Goodrum and Reid 1956). The literature on use of mesquite by wildlife was reviewed by Langford (1969).

Martin *et al.* (1951) listed the birds and mammals that use mesquite. They stated that since it is one of the few trees present in arid areas, its shade, though sparse, is welcome to wildlife and birds frequently nest in its branches.

In Arizona, mesquite constituted 36% of the diet of the antelope jackrabbit (*Lepus alleni*) and 56% of the diet of the black-tailed jackrabbit (*L. californicus*) (Vorhies and Taylor 1933). The rabbits especially ate the tufts of green leaves in the axils of the spines but also ate the leaves, bark, and buds. They cut off the lower branches of shrubby plants, making them less bushy. They ate mostly grass when it was green, and when it dried up they ate mostly mesquite. Norris (1950) found that both jackrabbits and desert cottontails (*Sylvilagus auduboni*) were most abundant on the most deteriorated rangeland in New Mexico, such as weedy areas and mesquite sandhills, and were least abundant in areas dominated by good grasses. Vorhies and Taylor (1933) believed that trimming of mesquite by rabbits promoted the recovery of mesquite dune areas, but there is little evidence that the dune areas are in fact recovering. Turkowski (1975) found that mesquite occurred in 12% of the stomachs of cottontails examined in Arizona and constituted only 2% of the quantity. Preference index for mesquite was only 0.64 in March through April, 3.21 in May through June, and 8.54 in December through February. Cottontail diets consisted of 43 species of identified plants.

Mares *et al.* (1977) listed 25 species of small mammals from mesquite communities in California, Arizona, and New Mexico. Mesquite made up 30% of the annual diet of the white-throated wood rat (*Neotoma albigula*) in Arizona. Mesquite and cactus complemented each other in its diet. When mesquite was available (February through April and July through October), consumption was high and consumption of cactus was high during the remainder of the year. The rats often stored mesquite pods and used them in nest construction. Wood rat populations averaged 11.9/ha, with a maximum of 51.1/ha (Vorhies and Taylor 1940).

In Texas, the pocket mouse (*Perognathus* sp.) ate more mesquite than any other plant; the pods made up 11.6% of its diet in winter and 13.6% in spring, and leaves 4.1% in winter and 12.5% in spring. For Ord's kangaroo rat (*Dipodomys ordi*), mesquite was third in importance; mesquite seed made up 8.0% of its diet in winter and 11.5% in spring, and leaves 4.7% in winter and 0.1% in spring (Alcoze and Zimmerman 1973). Mesquite seeds made up only 9.4% of the diet of Merriam's kangaroo rat (*D. merriami*), whose diet consisted mostly of grass seeds (Reynolds 1958). In Texas, rodent populations averaged 9.0/ha in mesquite associations (Blair 1943).

Mesquite makes up only a minor part of the diet of deer. In south Texas, honey mesquite ranked 11th on clay soils and 12th on sandy soils and constituted only 1–3% of the rumen contents of white-tailed deer (*Odocoileus virginianus*) (Drawe 1968). Forage ratings of mesquite were high only in June. Deer fed on 163 species of plants and 13 species made up 50% of their diet, so that no one species was of overriding importance.

Among browse plants, both huisache and blackbrush (*Acacia rigidula*) ranked ahead of honey mesquite as forage for white-tailed deer (Drawe and Box 1968). However, preference for mesquite was greatly increased by mowing or chopping (Powell and Box 1966). In the Big Bend area of Texas, mesquite constituted 5.8% of the rumen contents of white-tailed deer and 4.5% of mule deer (*O. hemionus*) in late summer; they did not feed on mesquite the rest of the year (Krausman 1978). In north Texas, frequency of honey mesquite in the diet of white-tailed deer varied from 1.7 to 9.8%; however, mistletoe, which often grows on mesquite trees, was the single most preferred food when available (Horejsi and Quinton 1973).

In Arizona, (velvet?) mesquite and *Acacia greggii* Gray together, mostly the beans, constituted 12% of the diet of white-tailed deer and 43% of that of mule deer in midsummer; they did not eat mesquite at other times of the year (McCulloch 1972). Anthony (1976), also in Arizona, found that the mule deer's diet was 2.2–7.5% mesquite but white-tailed deer did not eat any.

The pronghorned antelope (*Antilocarpa americana*) eats very little mesquite; in 3044 mins of feeding observed in the field, they fed only 6.2 min (0.2%) on mesquite (Buechner 1950). Feral burros (*Equus asinus*) in California ate a moderate amount of mesquite (mostly the beans), which made up 8.3% of the diet (Woodward and Ohmart 1976).

Several birds eat mesquite but most of them eat very little. However, the Gambel quail (*Lophortyx gambelii*) ate far more mesquite than any other food (Van Dersal 1938), although Martin *et al.* (1951) listed it as comprising only 10–25% of the diet. It was equal to deervetch as a food in the summer (18.8% of the diet) but was second to broomweed in the winter (Davis *et al.* 1975). The bob-white quail (*Colinus virginianus*) and the chestnut-bellied scaled quail (*Callipepla squamata castanogastris*) ate very little mesquite, 1.39% and 0.3% of their diet, respectively (Lehmann and Ward 1941). However, mesquite and shinnery oak were important quail habitats in northwest Texas (Webb and Guthery 1982).

Wild turkeys (*Meleagris gallapova*) also eat very little mesquite; it made up only 0.6% of the diet in the fall (Montei and Quinton 1973). Morning doves (*Zenaidura macroura*) near Las Cruces, New Mexico, apparently did not eat mesquite (Davis 1974). Although morning doves nested in honey mesquite trees in Mitchell County, Texas, they were more successful in ground nests where the trees had been burned (Soutiere and Bolen 1976).

Stamp (1978) stated that riparian woodlands are extremely important breeding places, wintering areas, and migration corridors for birds, but cottonwood (*Populus fremontii* S. Wats.) was much better habitat than mesquite. In a 40 ha cottonwood site near Phoenix, Arizona, she found 684 pairs of 28 species of birds and in a 40 ha mesquite site only 244 pairs of 19 species; only two species (four and eight pairs each) occurred in velvet mesquite and not in cottonwood and only one other species was more abundant in mesquite (60–56 pairs).

Most wildlife species within the distribution of mesquite thrive best in a varied habitat with adequate cover from brush or trees interspersed with open areas of grasses and forbs. The various systems for combining ranching with wildlife needs are discussed by Passey and Hicks (1970). Mesquite is of value as cover for wildlife in areas where other trees do not grow. However, in areas of mixed brush, other species are of greater cover value than mesquite (Inglis *et al.* 1978).

Plant Community

At present, mesquite (and other woody plants) provide safe sites against overgrazing by livestock for more palatable herbaceous plants. The removal of woody plants without proper grazing management can decrease the abundance of these plants to the point of no return (F.E. Smeins, pers. comm.). Biological or other methods of controlling woody plants must be followed by careful grazing management to preserve the community structure that includes these plants or else control may result in an undesirable deterioration in plant species diversity.

Nitrogen Fixation

Prosopis are legumes and all species presumably are capable of fixing atmospheric nitrogen through the symbiotic action of ***Rhizobium*** bacteria in root nodules. However, nodules have been found only rarely in the field and most searches have failed to find them. Felker (1979) lists several explanations that have been offered by various authors including absence of suitable rhizobia, presence of nodules only at certain moisture conditions, only at certain depths, or only at certain times during the growing season, and repression of nodule formation by high levels of nitrogen in the soil.

Recently, *Prosopis* has been observed to fix nitrogen under greenhouse conditions (Bailey 1976). Felker and Clark (1980) demonstrated nitrogen fixation in the greenhouse by 11 species of *Prosopis* (including two varieties of *P. glandulosa*) from Africa and North and South America. Roots of these species became nodulated when inoculated with a rhizobia strain isolated from the soil beneath a North American mesquite tree, and the plants grew on a nitrogen-free media and reduced acetylene to ethylene. Felker and Clark (1982) grew plants in 3-m-tall tubes in the greenhouse under simulated phreatophytic conditions in which they watered (after one initial watering) only at the bottom; many nodules were produced in the wet area at the bottom of the tubes but none closer than 2.7 m to the surface.

The demonstration of nitrogen fixation in the field is much more difficult and somewhat circumstantial, since nodules usually cannot be found and the acetylene reduction assay cannot be used. However, a few nodules were found and convincing circumstantial evidence of substantial nitrogen fixation was found in an area of the southern California desert, including a site near Harper's Well, where *P. glandulosa* was growing as a phreatophyte. Virginia and Jarrell (1983) recovered root nodules at a depth of 2 m from young mesquite plants growing in a moist wash near Harper's Well; they isolated a ***Rhizobium*** species from one nodule which was used to successfully nodulate plants in the greenhouse. Virginia *et al.* (1982), Virginia and Jarrell (1983), Jarrell *et al.* (1982), and Shearer *et al.* (1983) found that soil nitrogen in this area was 8–10 times greater under mesquite trees than between trees and was *c.* 10 times greater in the top 30 cm of soil than at the 60–90 cm depth. Rundel *et al.* (1982) and Shearer *et al.* (1983) calculated that they had found amounts of *c.* 1 kg N/m^2 in the upper 60 cm of soil beneath mesquite trees at Harper's Well. They concluded from measurements of the natural ^{15}N abundance in mesquite tissue relative to the ^{15}N abundance of soil N, and of the ratio of ^{15}N in mesquite tissue to that in presumed non-N_2-fixing plants, that much of this N had been symbiotically fixed by mesquite. They estimated that 43–65% of the N was fixed at six locations; however, at another location mesquite trees had not fixed any N. H.B. Johnson of this laboratory (pers. comm.) has also found evidence of substantial nitrogen fixation by mesquite at several sites in central Texas, by comparing ^{15}N ratios in tissues of mesquite and non-leguminous shrubs growing side by side.

A number of authors recently have accepted this evidence of nitrogen fixation from near Harper's Well as indicating that mesquite fixes large amounts of nitrogen wherever it grows and that this is of great importance in the environment (Gilbert 1982). I believe this assumption is premature. Shearer *et al.* (1983) stated that, prior to their work near Harper's Well under phreatophytic conditions, although *Prosopis* has the physiological capability of fixing N_2, there had been no convincing demonstration of large-scale N_2-fixation in the field. Felker *et al.* (1980), assuming nitrogen fixation, projected that pod yields of 4 tons/ha were possible for mesquite.

Gilbert (1982) hypothesized that clumps of mesquite trees, together with the grasses and other woody plants growing under them, act as 'slow-release tablets' that fix nitrogen and accumulate, protect, and slowly release nutrients back into the system. However, this system could operate with or without nitrogen fixation by mesquite since other organisms occurring there, such as herbaceous legumes, termites, and lichens also fix nitrogen. Also, many early records indicate that the grasslands were apparently in healthy condition before mesquite invaded, obviously without nitrogen from mesquite fixation. Gilbert (1982) further speculated that mesquite invasion of overgrazed rangelands in southern Texas might be a consequence of its nitrogen fixing ability which would give it a competitive advantage over other non-N-fixing plants. At the present time, there is little evidence to support this hypothesis.

Some of the explanation for high levels of nitrogen and other nutrients under mesquite trees may be concentration of nutrients under trees from the surrounding area (Tiedemann and Klemmedson 1973, 1977) by leaf fall, pod fall, dead branches and roots, and dung of perching birds and animals that nest or rest under trees, frass and dead bodies of insects that feed on trees, etc. This phenomenon may be as great or greater with some other species (such as *Celtis pallida* Torr.; Ulmaceae) than with mesquite (J.O. Klemmedson, pers. comm.). Secor *et al.* (1983) found much greater amounts of NO_3-nitrogen and smaller, but significant, increases in soil moisture, NH_4-nitrogen, phosphorus, calcium, and magnesium in surface soil under *Prosopis* and *Microrhamnus* (Rhamnaceae) shrubs than under *Quercus* (Fagaceae) and *Artemisia* (Asteraceae) shrubs in southeastern New Mexico. The observations that killing mesquite and non-leguminous woody plants both result in a sudden increase in grass production but for only 2–4 yrs, apparently resulting from release of nutrients held by the tree and its associated biota, seems to confirm that the increase is not dependent on nitrogen fixation by mesquite.

Aforestation

P. juliflora(?) plus indigenous *Prosopis* species have been successfully used for aforestation and erosion control in desert areas in Pakistan (Ahmed 1961; Ahuja *et al.* 1978; Muhammad 1952), India (Bhimaya *et al.* 1962; Choudhuri *et al.* 1979; Griffith 1939; Saxena and Singh 1976), Kuwait (Ellul-Micallef 1981), Abu Dhabi (Wood *et al.* 1975), Saudi Arabia (Abohassan and Randolph 1978), Libya (Anonymous 1969), Chile (Kirby 1972), and Hawaii (Esbenshade 1980).

In North America, mesquite has not been used for reforestation; in fact, the opposite seems to have occurred. Mesquite has invaded former grasslands and turned them into deserts (York and Dick-Peddie 1969). Nevertheless, mesquite may have some value for revegetation of mine spoils (Day and Ludeke 1980; Nowotny and Wood 1975; Verma and Ludeke 1977).

Potential for Biological Control

Several of the most successful projects on biological control of weeds have been against woody plants in rangelands and pastures. Examples are prickly pear cactus (*Opuntia* spp.; Cactaceae) in Australia, India, Sri Lanka, Celebes, South Africa, and Hawaii; lantana (*Lantana camara* L.; Verbenaceae) in Hawaii and Australia; hakea (*Hakea sericea* Shrader; Proteaceae) in South Africa; and manuka (*Leptospermum scoparium* Forester & Forester F.; Myricaceae) in New Zealand (Huffaker 1959; Goeden 1978; Julien 1982; Neser and Kluge 1985). Other examples of spectacular control are that of the American chestnut (*Castanea americana* [H. Marsh] Borkh.; Fagaceae) by an introduced fungus and of the American elm (*Ulmus americana* L.; Ulmaceae) by an introduced beetle and a fungus that it carries; the only difference is that we do not consider these plants to be weeds.

The method of introducing foreign insects is particularly useful in rangelands where the low production/unit area makes other control methods relatively expensive (Andres 1977; DeLoach 1981). The objective of biological control is not to eradicate the weed but rather to reduce its abundance to a level of lesser economic importance (Huffaker 1957, 1959). In the more than 100 previous projects attempted worldwide over a period of 120 yrs, no weed has approached eradication though several have been controlled at a sufficiently low level that no additional control by any method has been required (Goeden 1978; Julien 1982).

Prospects for controlling mesquite appear promising if conflicts of interest can be resolved. Ward *et al.* (1977) listed 657 species of phytophagous insects collected from mesquite in the U.S. and Mexico. These no doubt have a suppressing effect on mesquite but obviously have not been controlling the plant in recent years, although we might speculate that they did so before the introduction of livestock.

Additional insects (or other organisms) that could be introduced from another area of the world might provide added control here because they might: (1) fill a niche not fully exploited at present by the native insects; (2) if collected from a different but closely related mesquite species they might lack the homeostatic mechanisms that may have developed between native insects and mesquite; and (3) they may be able to escape injury by native parasites, pathogens and predators that attack the native insects. Each of these phenomena have occurred in other successful projects.

Cordo and DeLoach (*in press*) and other workers (Ward *et al.* 1977) in extensive explorations in Argentina and Paraguay have found over 300 species of insects that attack the 30 species of *Prosopis* that are native there. Of these insects, 39 species appear to be good candidates for introduction into North America for biological control. Of these, 14 species attack seed, 1 species flowers, 2 species buds, 11 species foliage, and 11 species limbs or trunks (Cordo and DeLoach, *in press*). the most promising appear to be 10 species of seed-feeding bruchid beetles in the genera *Rhipibruchus*, *Scutobruchus*, *Pectinibruchus*, and *Acanthoscelides* (all Coleoptera: Bruchidae); the first three of these genera are not represented in North America and all except one species appear to be restricted to *Prosopis* (Kingsolver *et al.* 1977). A seed-feeding weevil in the genus *Apion* (Coleoptera: Apionidae) causes heavy damage to developing seed in Argentina; such damage has not been observed here. Six species of small *Sibinia* (Coleoptera: Curculionidae) weevils that feed on buds and seeds cause damage in Argentina.

Among foliage feeders, gelechiid leaf tiers, from the genera *Evippe* and the *Recurvaria-Aristotelia* group (Lepidoptera: Gelechiidae) defoliated large areas of mesquite in Argentina; they attacked later in the season than the principal North American defoliator, *Melipolis indomita* (Walker), and the two would compliment each other. A geometrid, *Nephodia marginata* (Warren) (Lepidoptera: Geometridae), defoliated mesquite over large areas (Ward *et al.* 1977). Also, the bagworm *Oiketicus* sp., an unidentified noctuid, the sawfly, *Brachyphatnus* sp., and psyllids near *Euphalerus* sp. (Homoptera: Psyllidae) caused heavy damage (Cordo and DeLoach, *in press*).

Larvae of several beetles damage the trunks and limbs in Argentina. *Criodion cinereum* (Olivier), *Calocosmus morosus* White, *Alphus* sp. nr. *bruchi* Melzer, and *Ranqueles mus* Gounelle (all Coleoptera: Cerambycidae) bore in trunks and are known only from *Prosopis*. *Achryson undulatum* Burm., *A. unicolor* Bruch., and *Cyllene spinifera* Newman bore in branches and also are known only from *Prosopis*. The twig girdlers *Lochmaeocles sladeni* (Gahan) and *Odontocera flavicauda* Bates are known only from *Prosopis*; the former girdles branches up to 5 cm diam. which is much larger than those attacked by the North American twig girdlers. A tiny wasp, probably *Eschatocerus* *myriadeus* Kieffer (Hymenoptera: Cynipidae), was found occasionally; it caused the branches to burst open and die. Our field observations and review of the Argentine literature indicate that all of the above insects are probably specific to *Prosopis* but we have not yet done any host range testing. In addition, the insects are from genera that do not occur in North America, or at least are not known from *Prosopis* here (except for *Oiketicus* and *Apion*), and therefore have a reasonable chance of escaping North American parasitoids. Thus, they might be able to maintain higher populations and cause more damage than in Argentina. The type of stress produced on the plant can be selected by choosing the type of insect to be introduced, thus avoiding some conflicts of interest.

Of course, great care should be taken to introduce control agents that are host-specific to *Prosopis*. Since the North American weedy mesquites (*P. glandulosa* and *P. velutina*) do not occur in South America, natural enemies must necessarily be obtained from different species of *Prosopis* that are closely related. These control agents, therefore, necessarily will not be 'species specific' in host range and can be expected to feed on other North American mesquites in series Chilenses of the genus. The amount of feeding on non-target mesquite can probably be reduced by selecting species or biotypes of control insects that prefer *P. glandulosa* or *P. velutina*. The control insects should otherwise be safe because no other North American plants are closely related to *Prosopis*.

I would propose that some of the seed- and fruit-feeding insects should be introduced first. Huffaker (1959) suggested that seed-feeding insects probably would be ineffective in controlling weedy woody plants that reproduce by seed and produce large quantities of seed. However, Nesser and Kluge (1985) report that effective control of *H. sericea* in South Africa was being obtained by a seed-feeding weevil. Also, Harley (1985) reviews several programs where such control has been attempted and discusses situations where it might be successful. Seed-feeding insects theoretically would halt the spread of mesquite by lowering its reproductive rate and would not harm existing trees used for ornamentals, honey production, or firewood. Also, they would not harm the use of trees cultivated for energy production. Felker (1984) proposed that trees grown for biomass would have to be propagated vegetatively to maintain selected factors for high productivity; therefore, their propagation would not be affected by seed-feeding insects. Any use of mesquite pods and seed for animal feed would, of course, be affected. After a period of several years the biological control program should be re-evaluated to determine if the desired control was being obtained and decisions made as to whether additional insects should be introduced.

Conclusions

After reviewing the available literature, I conclude that the overall effect of biological control of mesquite would be beneficial. Present direct losses caused to the grazing livestock industry are probably $250–500 million annually in the U.S. plus a large amount in Mexico; this is probably 20–30 times the presently known beneficial values of mesquite. Total economic losses are about three times greater than direct losses. Soil erosion, desertification, and reduction of available soil water add greatly to these losses. Several of the suspected beneficial roles of mesquite probably are of minor importance, at least when compared with the great amount of harm caused. Historically, semi-arid rangelands throughout the world have been most efficiently utilized for grazing livestock and wildlife habitat. This condition will probably continue for the foreseeable future.

A few uses of mesquite have definite beneficial or potentially beneficial values. Cultivation of mesquite as a renewable energy resource in lieu of fossil fuels could be of great national value. However, the degree to which it could be exploited needs to be critically examined from the point of view of available water supply and economics of cultivation, harvesting, energy production, and alternative land uses. Presently, the method would appear to be restricted by water availability to small areas of high rainfall. The correspondingly high value of this land for agriculture would tend to preclude its use for mesquite production unless the intent is to grow it as an agricultural crop with irrigation (or on sites with available ground water), weed control, insect control, etc.

The possible value of mesquite for nitrogen fixation is an area of considerable uncertainty and of new research. It could be of great value in the ecosystem and to forage grasses as some workers speculate or it could be of little consequence. Recent research in California indicates that mesquite probably does fix nitrogen under certain conditions, such as when it grows as a phreatophyte. Also, recent analyses of ^{15}N ratios made by H.B. Johnson of this laboratory indicate that mesquite probably fixes substantial amounts of nitrogen in at least some upland sites in central Texas. Whether or not it fixes nitrogen in other areas and the amount fixed, requires further research. Nitrogen fixation in arid areas with a deep water table, or with no water table, may not occur or may be infrequent. The long-term experiments from New Mexico and Arizona indicate rather clearly that competition for water by mesquite is far more damaging to grasses in low rainfall areas than its combined beneficial effects. In central and eastern Texas, rainfall seems to be adequate for good growth of both grasses and mesquite, except in drought years. Long-term experiments are needed to determine if mesquite fixes nitrogen in this area, how much is fixed, and its importance in forage production and in the ecosystem.

The effect that a substantial reduction in the density of mesquite would have on subsistence cultures needs clarification. Control of mesquite would in inappropriate if these peoples were deprived of a way of earning a suitable livelihood. However, a good possibility exists that other trees such as huisache could provide sufficiently for firewood, farm implements, and household industries, and that a reduction in mesquite density would allow greater forage production for their livestock also.

Mesquite appears to have little potential as human food except as a novelty food and perhaps as a ceremonial food in certain Indian tribes. It is, however, of considerable value as a nectar source for honey production. Substantial control would result in some loss of production and relocation of bee colonies to other areas.

A substantial one-time loss of ornamental shade trees could occur if foliage-feeding or limb- and trunk-feeding insects were introduced for biological control; however, very few homes have mesquite as the only shade tree. Public displeasure over the damage of shade trees would be diminished because the major use occurs in zones where the damage caused by mesquite is a major public concern. Some, though certainly not all, shade tree owners would be willing to accept damage in order to have the rangeland problem improved. Damage to shade trees could be avoided if only flower-, pod-, or seed-feeding natural enemies were introduced.

Mesquite appears to have little potential for commercial utilization in livestock feeds in the U.S. The foliage is mostly unpalatable and the cost of converting the wood into feed is too great. Livestock highly relish the pods when ripe but low and erratic production lowers their value for feed, the seed are not digested so most of the protein is lost, and too great an intake results in digestive problems. The cost of harvesting and processing the pods makes them uncompetitive in cost with commercial feeds.

Mesquite wood is used for firewood, barbecue wood, and for handicrafts. Mesquite barbecue wood is now popular but this specialized market may or may not continue in popularity. Biocontrol is unlikely to eliminate so much mesquite that wood for firewood or for crafts would become scarce.

Many chemicals have been identified from mesquite but few have been used in medicine or industry. Tannin from mesquite is not of high enough concentration or quality to compete with that from other sources. Gums are of good quality and could substitute for gum arabic but harvesting is expensive and mesquite gum cannot compete in cost with imported gums. Alcohol can be produced from mesquite, but cannot compete economically with that from cereal grains or sugar crops.

Some of the harmful and beneficial effects of mesquite are not sufficiently documented. Areas that need special attention are loss of grass caused in regions of higher rainfall, direct measure of losses in livestock production, better data for economic analyses, and possible value of mesquite in nitrogen fixation. Also, the large literature on its value for wildlife food and cover needs to be summarized and more research may be needed, especially of non-game species. Whitson and Scifres (1979) observed that little brush control research had been done in Texas to evaluate long-term production response because: (1) most tests measured only response of target species to treatment with little regard to the forage component; (2) plots were too small to evaluate forage/animal performance or results were confounded with land-use patterns of cooperating ranchers; and (3) long-term response data has not been possible because of cost, personnel changes, and short-term goals. Gilbert (1982) rightly criticized much of the forage-brush control research, especially in Texas, as suffering 'from insufficient duration (many are 2-year master's degree projects) and only evaluate the end agronomic result (production of grass or livestock) without investigating details.' I would join them in calling for long-term, high-quality ecological research in the more humid zone where mesquite grows, particularly to discover the importance of mesquite in the rangeland ecosystem as a basis for re-evaluating existing range management procedures; such research recently was begun by H.B. Johnson of our laboratory at Temple, Texas. Some excellent long-term work has been done in the western areas (the Santa Rita and Jornada Experimental Ranges) but more is needed.

In my opinion, a substantial reduction in the abundance of mesquite would have minimal adverse effects on the ecosystem and might even be balanced by some beneficial ecological effects. Mesquite is many times (possibly 50–100 times) as abundant now as before the coming of western man and its density is still increasing; 80–90% control would not even return mesquite to its 'original' density of 150 yrs ago. A substantial reduction by biological control would promote the return of the 'mesquite dune' areas to their former status of desert grasslands. This beneficial effect assumes that rangelands would not be seriously overgrazed by livestock.

Populations of jackrabbits and several rodent species have increased to abnormally large populations as mesquite has increased and they now contribute to continued deterioration of grasslands. Mesquite control would help reduce populations of these species to more 'natural' levels. Gambel quail populations would probably be reduced if mesquite were substantially controlled; however, it is very unlikely that the species would be seriously harmed. Other birds and mammals, including deer, do not depend enough on mesquite to be harmed by a substantial mesquite reduction. The extent to which reptiles and invertebrates would be affected by mesquite control is not known.

Johnson (1985) addresses in depth the questions concerning the control of a major native member of the plant community on ecosystem function. Past records indicate that, even in cases of catastrophic reductions of dominant native species, recovery was rapid and the ecosystem remained healthy, although the position of the one species affected changed greatly. Also, in all cases of major successes in biological control of weeds, low populations of the weed remain even in the area of greatest control and in outlying areas of slightly differing climate the weed is relatively abundant. He concluded that theory that follows the individualistic concept of community structure proposed by Gleason (1939) more properly describes natural processes, and allows ecosystem stability based on functions that are independent of species composition, than the more popular Clementsian theory based on the concept of a fixed and delicately balanced species composition of climax vegetation.

This review of mesquite literature, which is also a dominant native plant over a large area, indicates that substantial reduction in abundance also would probably have minimal adverse effects in the ecosystem. I suspect that thorough investigation would also reveal that minor, non-target, native plant species, although part of a natural plant community, play a minor role in the ecosystem and have little likelihood of being driven to an endangered status or to extinction by introduction of biocontrol agents. Density-dependent mechanisms would act to prevent over-exploitation of these species that exist at low densities. Although the concern that we should not inadvertently wreak havoc with the ecosystem by introducing foreign organisms to control native plants is worth very serious consideration, there is little or no evidence either in accepted ecological theory or in case histories to indicate that this would happen.

Given the great genetic diversity of mesquite and diversity of climate and soil of areas where it grows, it almost is inconceivable that a catastrophic reduction in mesquite density would occur with introduction of one or a few natural enemies. The most probable scenario is that several insects would have to be introduced in sequence to gradually reduce stands of mesquite, and more than 75–80% final control seems unlikely. Introductions could cease when an acceptable level of control was reached.

Successful biological control of mesquite appears technically feasible with the insects known in Argentina. Control could result in greatly increased livestock production at less cost for weed control, which would greatly benefit the ranching industry and the associated economy that depends on the ranching industry. However, damage would occur to certain users of mesquite, the degree depending on the type of insects introduced. These conflicts of interest between persons and groups who regard mesquite as harmful and those who regard it as beneficial are economic and socio-political and must be resolved at that level. A biological control program could proceed rapidly once these questions are resolved.

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Biological Control of Blackberries: Resolving a Conflict in Australia

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Abstract

European blackberry (*Rubus fruticosus* agg.) is an important pastoral and forest weed in high rainfall areas of south-eastern Australia. Foreign exploration for control agents commenced in 1978, but apiarists and berry canners opposed attempts to have blackberry approved as a candidate for biological control. This forced the need for extensive economic analyses on the impact of the weed on agriculture. Costs associated with blackberry were found to exceed $40 million annually whereas benefits were less than $1 million. Concern was also expressed over the biological control agent, the rust *Phragmidium violaceum*. Berry farmers saw the programme as a risk, even prior to the completion of specificity tests; however, graziers threatened to illegally import the rust if the programme halted. Specificity tests on the rust were completed in March 1983, but in February 1984, before the conflicts were resolved, the rust was recorded in Victoria.

Lutte Biologique Contre les Ronces — Résolution d'un Conflit en Australie

Les ronces (*Rubus fruticosus*) sont des plantes nuisibles pastorales et forestières importantes dans les zones de fortes précipitations du sud-est de l'Australie. En 1978, on a commencé à chercher des agents de lutte biologique contre ces mauvaises herbes à l'étranger. Cependent, les apiculteurs et les exploitants de conserveries de petits fruits se sont opposés à la lutte biologique contre les ronces, d'où la nécessité de faire des analyses économiques d'envergure sur les effets de ces plantes nuisibles sur l'agriculture. Les analyses ont permis de déterminer que les coûts d'élimination des ronces dépassaient 30 millions de dollars par an, tandis que les avantages tirés de ces plantes nuisibles étaient de moins de 1 million de dollars par an. Des préoccupations ont également été soulevées au sujet de l'agent biologique choisi, à savoir la rouille *Phragmidium violaceum*. Les propriètaires des exploitations de petits fruits jugeaient que le programme comprenait trop de risques, même avant la fin des essais de spécificité; toutefois, les exploitants de pâturages ont menacé d'importer illégalement la rouille si le programme était interrompu. Les essais de spécificité sur la rouille ont pris fin en mars 1983 mais, en février 1984, avant que les conflits ne soient réglés, la rouille a été relevée à Victoria.

Introduction

The procedure for introducing biological control agents for weeds into Australia has been under review since the late 1970s. The need for a procedure that formally addressed all potential conflicts associated with a given weed became evident when a High Court injunction, taken out by apiarists and graziers, prevented the CSIRO from releasing insects to control *Echium plantagineum* (L.) (Boraginaceae). A procedure was developed requiring submissions from all States on the importance of the candidate weed. In particular, submissions were to contain as much economic information as possible and identify any beneficial attributes that may cause a conflict of interest. Unanimous agreement between States was necessary before a weed could be declared a candidate for biological control.

This procedure was fully adopted in 1980, one month after the High Court injunction on CSIRO was granted. Whilst this protocol may identify potential conflict areas and halt programmes before costly foreign exploration work commences, it would not overcome legal challenges to programmes at a later time. Legislation has now been drafted and, if enacted, will limit the opportunity for legal action. This is dealt with more fully by Cullen and Delfosse (1985).

In Victoria, blackberry (*Rubus fruticosus* L. agg.; Rosaceae) is probably the most costly declared noxious weed. The most common chemical used to control it has been, and still is, 2,4,5-T ([2,4,5-trichlorophenoxy] acetic acid). Through the mid-1970s there was mounting public concern over the side effects of 2,4,5-T. This concern, along with the importance of blackberry to Victoria, and the recent success in biological control of blackberry in Chile (Oehrens and Gonzalez 1974, 1977), resulted in the commencement of a programme in Australia. Bruzzese (1980*a*, *b*) surveyed *Rubus* spp. in Victoria and recorded the phytophagous arthropods and diseases attacking the plants, and then in 1978, commenced similar surveys of *R. fruticosus* in Europe. By 1980 the rust *Phragmidium violaceum* (C.F. Schultz.) Winter (Uredinales), the disease introduced into Chile, and the stem-boring sawfly *Hartigia albomaculatus* (Stein) (Hymenoptera: Cephidae) were identified as the most likely potential control agents of blackberry.

The specificity tests on *P. violaceum* and *H. albomaculatus* had commenced when the procedure for having weeds declared candidates for biological control was approved by all State Ministers for Agriculture. This paper describes the nature of the conflicts of interest which arose during the early stages of the programme, the economic analyses undertaken to demonstrate the high cost of blackberry to Australia, and the means by which the programme proceeded without the conflicts being finally resolved.

The Candidate

The native range of *R. fruticosus* agg., is Europe, the Middle East and north-west Africa. *R. fruticosus* now also occurs in North America, Chile, South Africa, Australia and New Zealand, mainly in areas where the annual rainfall exceeds 760 mm and in the latitudes 30° to 65° N and 28° to 40° S (Amor and Richardson 1980). In Australia it occurs in all States except the Northern Territory. It is considered an important weed in New South Wales, Victoria and Tasmania, of lesser importance in South Australia, and of minor importance in Queensland and Western Australia. It is proclaimed under noxious weeds legislation in all States.

In Australia blackberry is an important weed of native bushland, commercial forestry operations and agriculture. The plant forms dense, prickly thickets, commonly 1 to 2 m high, that harbour vermin and are impenetrable to man and his domestic animals (Amor and Richardson 1980). Most of the blackberry in Victoria is in native forest. Dense infestations reduce plant diversity and limit access to streams for recreational purposes and the watering of stock (Amor and Harris 1979). On agricultural land blackberry excludes pasture, and sheep can become entangled in the canes. Whilst bushes are not grazed by either sheep or cattle, goats preferentially graze the plant and do reduce plant vigour.

Control of blackberry is difficult, particularly in hilly terrain where access by ground vehicles is poor. The most common control method is to spray with the herbicide 2,4,5-T but this chemical usually does not provide complete control even after two applications in the one season (Amor 1975). Alternative chemicals, although often more effective, are generally more expensive or have other drawbacks such as greater soil persistence.

Other control practices include mowing several times a year but this will only suppress and not eradicate the weed (Amor and Richardson 1980).

In 1975 there was an estimated 663,000 ha of land infested with blackberry in Victoria (Amor and Harris 1979). In 1981/82 the Government spent about $0.25 million on herbicides which cost $1.25 million to apply to blackberry on Crown Land. During that same year it sold to private landholders $0.267 million of herbicides for the control of blackberry. A further amount of $0.267 million is estimated to be purchased by landholders from non-Government sources.

In New South Wales blackberry is a significant weed of the tablelands and slopes and covers nearly 4,000,000 ha, although three-quarters of these infestations are sparse. The estimated total (State and private) expenditure on blackberry control in New South Wales in 1980 was $4.94 million (Mears 1981).

Blackberry does have some beneficial qualities. Approximately 100 tonnes of wild blackberry fruit is used commercially every year for producing blackberry jam in Victoria (Amor and Richardson 1980), and some jam-making also occurs in Tasmania and New South Wales. Apiarists utilize blackberry as a pollen and nectar source, the Tasmanian apiarists deriving more benefit from the plant than those from the mainland States. Before the weedy potential of the plant was recognized, blackberry was used to reduce soil erosion on creek banks, but more appropriate alternative plants are available for this (Amor and Richardson 1980). Some members of the *R. fruticosus* agg. have also been used in North America in breeding programmes for cultivated berry varieties, some of which are grown in Australia.

Despite an extensive spraying programme to control blackberry in Victoria and New South Wales over many years, there is every indication that infestations are increasing in these States (Amor and Richardson 1980; Mears 1981). However, the inaccessibility of many of the infestations and the restrictions on the use of aerially-applied herbicides make treatment difficult. Biological control would be an ideal method of containing the spread of this weed.

The Conflict

Opposition and concern about the biological control programme came from three main areas: apiarists, pickers and canners of wild berries, and growers of *Rubus* crops.

Apiarists

Blackberry is a useful plant in apiculture because of both its nectar and pollen production; however, its importance is almost entirely confined to Tasmania. In this State bees work both blackberry and clover at the same time, producing a high quality, white honey. The relative importance of the clovers (*Trifolium repens* L. and *T. pratense* L.; Leguminosae) and blackberry is unknown, although blackberry is a more reliable source, particularly in dry years, and could account for up to 90% of this honey type.

Blackberry is also considered important as it increases hive populations prior to the flowering of the leatherwoods (*Eucryphia lucida* Baillon and *E. milliganii* Hook.; Eucryphiaceae), which is the apiarists' most valuable crop in that State, contributing from 37–80% (average 57%) of the honey yield in the years 1973–78 (Anon. 1979). The value of blackberry in hive build-up is difficult to estimate but, if artificial food (candy made from sugar) was used to replace blackberry nectar it would cost approximately $5.00/hive for the 12,000 Tasmanian hives; i.e. $60,000/year. Furthermore, if blackberry is considered to account for 80% of the non-leatherwood honey, then the average annual value of this honey would have been $163,000 for the years 1973–78. Add to this the contribution blackberry makes to larger hives for the collection of leatherwood nectar and the total value of blackberry to Tasmanian apiculture becomes $223,000 (Table 1). Of the 57 apiarists in Tasmania with 40 or more hives in 1979–80, 10 accounted for more than 82% of the honey production (Anon. 1980).

The Tasmanian apiarists are, therefore, opposed to any programme of biological control of blackberry; mainland apiarists are less concerned.

Table 1. Benefits and costs of blackberry in New South Wales, Victoria and Tasmania.

State	Enterprise/Location	Benefit ($)	Cost ($)
New South Wales	Agriculture		20,000,000
	Forestry		400,000
	Crown Land		556,000
			20,956,000
Victoria	Agriculture		
	- Lost production on:		
	unsprayed land		3,115,582
	sprayed land		4,673,372
	- Chemical costs		
	(all sources)		534,849
	- Labour		3,336,950
			11,660,753
	Forestry		20,000
	Crown Land		1,675,350
			1,695,350
	Berry Collection		
	- Commercial	240,000	
	- Private	57,500	
		297,500	
Tasmania	Agriculture		6,500,000
	Crown Land		60,000
			6,560,000
	Agriculture		
	- Honey	163,000	
	- Hive build-up	60,000	
		223,000	
	Berry Collection		
	- Commercial	120,000	
	- Private	17,500	
		137,500	
	TOTAL	$658,000	$40,872,103

Collectors and Canners of Wild Berries

The major value of the fruit as a food is for jam manufacture. Because of the distinctive flavour of wild berries they are used in a 1 in 2 or 1 in 3 blend with cultivated berries. The collection of berries occurs mainly in Victoria (67%) and Tasmania (33%). The amount processed each year is variable and appears to be declining. New varieties of cultivated blackberries and importations of berries from New Zealand, both wild and cultivated, are replacing the use of wild berries from Victoria.

The estimated value of wild blackberries picked for processing is $360,000.

Berries are also collected by individuals for home consumption and for sale on the fresh fruit market. The total value of such berries is unlikely to exceed $75,000 (equivalent to 75 tonnes of fruit); however, no accurate figures are available.

Some commercial berry processors were concerned that a biological control programme would reduce their intake of wild berries and some individuals who derive income from the collection of berries are also opposed to any biological control programme. The total estimated value of wild blackberry fruit is $435,000 (Table 1).

Growers of Rubus *Crops*

During the process of consultation to achieve concensus between States, concern was expressed regarding the specificity of the likely biological control agent, *P. violaceum*. This confused the issue regarding the candidacy of blackberry to the extent that prejudgement on the specificity resulted in some opposition to the programme. For the same reason the New Zealand berry industry was apprehensive about the programme as any rust introduced to Australia was likely to be blown across the Tasman Sea, 2,000 km to New Zealand.

The Resolution

In Tasmania, the costs associated with blackberry in terms of lost agricultural production and cost of control, was considered to be between 4 and 20 times the benefits derived from the plant. But because that State has an important cultivated berry industry, the State Government decided not to support blackberry being declared a candidate for biological control. However, in some mainland States, in particular Victoria and New South Wales, the initial calculations for the cost of controlling blackberry alone, that is without accounting for lost agricultural production, was at least 10 times the benefits derived from the plant. Overall, the importance of blackberry as a cost to the nation dwarfed the benefits derived from within Tasmania and Victoria.

Following a change in the Tasmanian State Government, the attitude taken was re-assessed. The State no longer opposed the proposal that blackberry be declared a candidate for biological control but, stipulated that a substantial improvement was required in the economic analysis undertaken by the mainland States. However, the apiarists and berry collectors still remained totally opposed to the programme.

In Victoria, the economic analysis attempted to determine the value of lost agricultural production. The analysis was based on a number of assumptions, usually quite conservative, and relied heavily on information supplied by government field officers. These officers are a major outlet for the sale of herbicides in Victoria and supplied receipts from these sales which provided information on the type and amount of herbicide, weed to be controlled, name and address of the purchaser, and the cost. Receipts from all sales relating to blackberry were collated on a District basis. Herbicide sales for the control of blackberry occurred in 94 of the 139 Districts (Fig. 1). The sales of each chemical and the estimated area treated are shown in Table 2. Total sales for 1981–82 amounted to $267,424.

The main assumptions used in the analysis were: (1) all herbicide purchased for blackberry control was sprayed only on blackberry in that year; (2) all herbicides were applied at the recommended rates; (3) only one application of herbicide was made to each blackberry patch that year; and (4) the area sprayed on each property was considered to be totally unproductive, but capable of producing returns equivalent to the District average for the enterprise operating on that farm.

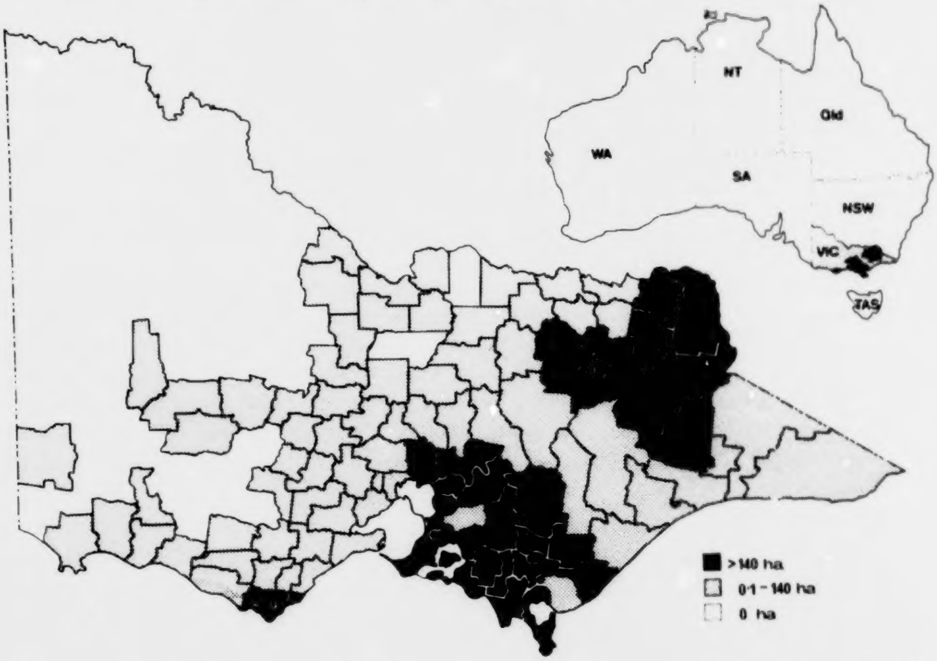

Fig. 1. Areas of dense blackberry infestations on agricultural land in Victoria sprayed with herbicides purchased from the Government.

From the recommended rates of use of each chemical, the area of densely infested blackberry on private property was calculated. From the receipts for the 29 most heavily infested Districts (Fig. 1) the government officers were able to identify the enterprise affected by the weed on each property. These Districts constituted 77.3% of the State's private land sprayed for control of blackberry with herbicide purchased from the Government.

The 29 Districts were then analysed to determine the value of lost agricultural production. Information on stocking rates and gross margins (gross returns less variable costs) for the major enterprises were obtained for the relevant Districts (Kinsella 1980; Trapnell 1982; McRae 1983). These enterprises occurred on 79% of the sprayed land. For the purpose of the analysis, the other 21% was considered not to be suffering economic loss. This land was used for hobby farms and enterprises such as piggeries, nurseries, poultry farms, orchards, pine plantations and even apiculture! The estimated value of lost production from the 29 Districts was $1,805,115, 68.5% of this on land used for dairying (Table 3). Assuming that the other 65 Districts have the same enterprises at similar stocking rates to the average of those analysed, a further cost of $531,570 would occur. Therefore, the total cost of lost agricultural production from this source of herbicides becomes $2,336,686. Estimates from private company sales suggest that non-Government sources supply about 50% of the 2,4,5-T used on blackberry. The actual sprayed area in Victoria would, therefore, be twice that calculated above, and thus the total loss of production on sprayed land is estimated to be $4,673,372 (Table 1).

Amor and Harris (1979) reported that only 60% of the agricultural blackberry is sprayed annually. If the other 40% is capable of producing returns similar to the sprayed areas, a further $3,115,582 is lost, bringing the total loss of production in Victoria to $7,788,954. To this value can be added the cost of spraying blackberry (chemicals and labour but not machinery costs) estimated to be $3,871,799 when all sources of herbicide are considered. The total estimated cost to Victorian agriculture is, therefore, $11,660,752 (Table 1).

Table 2. Chemicals sold to landholders for control of blackberry by the Government and estimates of the areas sprayed (1981/82).

Chemical	Volume (L)	Area sprayed (ha)	Chemical Cost ($)
2,4,5-T 40%	43,299	8,027.1	181,855.80
2,4,5-T 80%	673	249.3	5,552.25
amitrol	11,519	192.8	24,765.85
picloram +2,4-D	1,885	31.4	21,960.25
glyphosate	1,600	53.1	25,600.00
hexazinone[1]	365	-	5,584.50
triclopyr	81	12.9	2,106.00
TOTAL		8,566.6	$267,424.65

[1] Area not included because used for total vegetation control.

Other known costs in Victoria associated with the control of blackberry include $1,529,000 spent by the Government on public and forest land and $20,000 spent by private foresters. However, all costs incurred in forestry operations are not known, nor was it possible to place an economic value on the loss in forestry production or the loss to the national heritage when blackberry infests native forests and national parks. In conclusion, the total cost of blackberry to Victoria is in excess of $14 million annually.

The economic analysis undertaken in New South Wales was confined to a detailed study of the Central Western region. Here an estimate of the potential wool production forgone during the 1982–83 season was $4,251,000 and Vere and Dellow (1984) estimated this cost would be substantially larger on a State basis and might be as high as $20,000,000.

In summary, the known costs associated with blackberry are about 60 times the benefits derived from the weed (Table 1).

The concern of the Tasmanian apiarists and berry collectors became known in mid-1983 when their case appeared nationally on television. However, there was also considerable moral support from individual graziers for the continuation of the blackberry programme. Many threats were made both verbally and in writing stating that the rust, *P. violaceum*, would be illegally introduced into Australia, from either Chile or Europe, if the programme was halted.

Host-specificity tests on the rust were completed in France in April 1983 but the economic analyses were not completed until the middle of 1983 (Victoria) and early 1984 (New South Wales). In February 1984 residents of Hiawatha Valley near Yarram, Victoria, submitted specimens of blackberry leaves to the Forest Commission claiming they showed evidence of herbicide spraying in the area. The leaves were found to be infected with *P. violaceum* (Marks *et al.* 1984). A number of other foci of infection were later found in Victoria, suggesting that the rust had been deliberately introduced to these sites within the previous few months.

Table 3. Value of lost agricultural production[1] in Victoria for major enterprises in 29 Districts heavily infested with blackberry (1981/82).

Enterprise	Areas sprayed (ha)	% of total area	Value of agricultural production	% of total value
Dairy	2,100.88	40.0	1,236,277.50	68.5
Beef	1,833.08	34.9	218,339.28	12.1
Sheep (lamb/wool)	417.92	8.0	76,289.94	4.2
Mixed grazing	629.86	12.0	86,626.82	4.8
Vegetables (plus potatoes)	164.74	3.1	179,565.24	9.9
Cattle/tobacco	101.44	2.0	8,016.89	0.5
TOTAL	5,247.92	100.0	$1,805,115.67	100.0

[1] Derived from the area sprayed with herbicides purchased only through the Government. Values derived from gross margin estimates for enterprises in each District.

Conclusion

Although *P. violaceum* now occurs in Australia and is spreading rapidly (Bruzzese and Field 1985), the conflicts surrounding the programme still remain. The effectiveness of the introduced strain(s) of the rust on the noxious blackberry taxa is still largely unknown. If some of the species are resistant to the rust there may be a need to import the tested strains from France. To do this, blackberry will still have to become a declared candidate for biological control and this will no doubt require a public enquiry when the proposed legislation is enacted.

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Conflicts in the Use of Plant Pathogens as Biocontrol Agents for Weeds

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Abstract

Theoretically, plant pathogens are ideal candidates as biocontrol agents for weeds. However, their use is subject to the same conflicts of interest that are encountered with other biocontrol agents. Namely, what will be the effects of their use on non-target species and what will be the eventual long-term influence on agro- and natural ecosystems. Despite their relatively recent usage as biocontrol agents, conflicts have already arisen and others, real or imagined, are certain to follow. Indeed, many of the same attributes, such as host range and reproductive capacity, that make pathogens ideal biocontrol agents can also serve to change them from friend to foe. Ironically, so can the whims of mankind. Examples of the types of conflicts of interest will be discussed in this presentation.

Conflits d'Intérêts Concernant l'Utilisation d'Agents Pathogènes pour la Lutte Biologique Contre les Plantes Nuisibles

De façon théorique, les agents pathogènes des plantes constituent des candidats idéals pour la lutte biologique contre les plantes nuisibles. Toutefois, leur utilisation soulève les mêmes conflits d'intérêts que lorqu'on emploi les autres agents biologiques: quels seront les effets de leur utilisation sur les espèces non visées et les répercussions à long terme sur les écosystèmes agricoles et naturels. Bien que l'utilisation des agents pathogènes en vue de la lutte biologique soit relativement récente, des conflits ont déjà surgi et d'autres, réels ou imaginés, vont certainement suivre. En effet, de nombreuses caractéristiques comme la gamme d'hôtes et la capacité de reproduction, qui font de ces agents pathogènes d'excellents agents de lutte biologique, peuvent également faire de ces amis des ennemis. Par ironie, les lubies de l'homme peuvent en faire autant. Les auteurs donnent des exemples du genre de conflits d'intérêts provoqués par les agents pathogènes.

Introduction

Plant pathogens have many desirable characteristics that make them ideal candidates as biocontrol agents for weeds (Freeman *et al.* 1974; Zettler and Freeman 1972). Therefore, it is surprising that prior to 1970, little concentrated research had been focused on their use for such purposes (Wilson 1969; Zettler and Freeman 1972). However, since 1970, there has been a dramatic increase in research efforts directed toward the incorporation of plant pathogens into biological control programs for both aquatic and terrestrial weeds (Charudattan 1978; Freeman and Charudattan 1981; Templeton 1982). As one would expect, with this increase there has also been increasing awareness of conflicts, both real and imagined, that may accompany their usage.

Andres (1981) discussed conflicting interests that may arise in the use of biological agents for weed control. He categorized them into economic, ecological, and aesthetic conflicts. Although his discussion dealt primarily with insects, use of plant pathogens as biocontrol agents is subject to the same categorical conflicts. Harris (1980) has pointed out that biological control research is still dependent upon an empirical element. Because of its more recent development, this is especially true in research on plant pathogens. The injection of such an element into scientific research certainly increases the potential for conflicts to arise — and they have. Some are imagined, but others are real. In addition, because of the potential for genetic diversity noted by Leonard (1982), conflicts may be even more frequent with the use of pathogens than other biotic agents. There are also other factors that form a basis for conflict. It is the purpose of this presentation to discuss the theoretical aspects that may lead to conflicts of interest in the use of plant pathogens in the classical and bioherbicidal approaches to controlling weeds biologically and to cite specific conflicts that have already occurred.

Conflicts in the Classical Approach

As defined by Tisdell *et al.* (1984) 'Classical biological control involves the release of a natural enemy (predator, parasite) of a weed or pest. The biocontrol agent is imported and once established, the population of the agent is self-sustaining and reaches a long-term equilibrium with that of its (weed) host'. Harris (1980) cites several examples, dating back to the turn of the century, of the use of insects in the classical approach to biocontrol of weeds. There have also been some notable successes with exotic plant pathogens. They are: the use of *Puccinia chondrillina* Bub. & Syd. (Uredinales) for control of *Chondrilla juncea* L. (Compositae) in Australia (Cullen 1974; Cullen *et al.* 1973; Hasan 1974), and the western United States (Emge and Kingsolver 1971; Adams and Line 1984); control of *Ageratina riparia* (Hyphomycetes) (Regel) R.M. King & H. Robinson in Hawaii with *Cercosporella riparia* (Trujillo 1976); and control of *Rubus* spp. (Rosaceae) in Chile with the rust *Phragmidium violaceum* (Schultz) Winter (Uredinales) (Oehrens 1977).

Thus far, no serious conflicts have arisen in the successes cited. True, the potential is there. For example, in Australia, three ecotypes of rush skeletonweed varying in their resistance to *P. chondrillina* apparently existed when the pathogen was released (Hull and Groves 1973). Following the successful establishment of *P. chondrillina* as a biological control agent, a decline in the numbers of the predominant host type that was susceptible to the rust and an increase in the numbers of two other resistant host types occurred in some areas where they were present (Burdon *et al.* 1981). Also, *P. violaceum* can affect cultivated *Rubus* spp. The present status of this pathogen in Chile is not known, but no adverse effects have thus far been reported.

Despite the lack of documented serious conflicts, there is an air of pathophobia that has brought to a virtual standstill the application of the classical approach in the use of plant pathogens for weed control. As far as we can determine, *P. chondrillina* is the first and the only exotic plant pathogen approved for release in the continental United States. In Florida, the proposed release of *Uredo eichhorniae* Gonz.-Frag. & Cif. (Uredinales) (Charudattan and Conway 1975), a rust pathogen of waterhyacinth (*Eichhornia crassipes* [Mart.] Solms-Laubach; Pontederiaceae) and Araujia mosiac virus (Charudattan *et al.* 1980) a pathogen on milkweed vine (*Morrenia odorata* [Hook. & Arn.] Lindl.; Asclepiadaceae), a serious weed in citrus groves, was rejected by the U.S. Department of Agriculture. The former because of lack of documentation of an alternate host, if one exists, and the latter because of an unsolvable conflict concerning its possible pathogenicity on certain 'endangered' species in the milkweed family (Asclepiadaceae) thought to occur in Florida. Prior to its disapproval, Charudattan *et al.* (1980) and Charudattan and Heron (1982) had tested the virus against 121 plant species in 25 different families. Only 10 species of milkweed, all vines, were susceptible. None of the herbaceous milkweeds tested was susceptible. Also, in the Florida program, two other exotic pathogens of waterhyacinth were tested and rejected by the investigators because of their wide host range. One was *Bipolaris oryzae* (previously identified as *B. stenospila* Drechs.; Hyphomycetes), isolated from waterhyacinth in the Dominican Republic (Charudattan *et al.* 1976) that was also pathogenic on rice (*Oryza sativa* L.; Gramineae), sugarcane (*Saccharum* spp.; Gramineae) and burmudagrass (*Cynodon dactylon* [L.] Pers.; Gramineae). Ironically, bermudagrass is listed by Holm *et al.* (1977) as the second most important weed in the world. Not so in Florida where tourists play millions of rounds of golf on more than 900 golf courses planted with bermudagrass. The second pathogen was a *Rhizoctonia* sp. (Hyphomycetes) from Panama (Freeman and Zettler 1971) that was also pathogenic to a large number of crop species. The work with this pathogen was suspended despite the fact that *Rhizoctonia* spp. are ubiquitous in soils throughout the world. *Rhizoctonia* sp. has also been reported to affect desirable aquatic plants (Bourne and Jenkins 1928). Hence, work with this exotic fungus was abandoned and was not resumed even when it was later found naturally occurring in the United States (Freeman *et al.* 1981).

To minimize conflicts that may arise in the use of exotic pathogens, two approaches have been taken to insure their safety. Australian efforts have been directed towards studying the host range and biocontrol potential of the organism in areas where it and the target weed are native. This approach is the safest in the initial phases. However, it has limitations in that it may not be possible to thoroughly test host range on plant species, biotypes, and varieties native to the target area. In the United States, pathogens have been introduced into quarantine facilities where their biocontrol potential and host range have been evaluated. This method has an advantage in that plants native to the target area can be more thoroughly tested. However, it has the disadvantage of the possibility of escape of the organism through human error or damage to the quarantine facility caused by natural disaster. Therefore, both approaches have limitations that could lead to unforeseen conflicts.

It should be noted that plant pathogens throughout the ages have found their way from country to country and continent to continent. Just as with weeds, man is usually the culprit in their transportation from place to place. For example, *Puccinia xanthii* Schw. was accidently introduced in Australia from the United States. It became established in Australia on *Xanthium* spp. (Compositae), and has since been found to parasitize at least two varieties of sunflower (*Helianthus annus* L.; Compositae) (Tisdell *et al.* 1984). However, natural forces can also move pathogens. Coffee rust, *Hemileia vastatrix* Berk. & Br. (Uredinales), is believed to have been carried by wind currents from Africa to South America and annually cereal rust spores are carried by wind currents from Mexico and the southern United States along the 'puccinia pathway' into Canada. Thus, despite our most elaborate efforts, we must realize that movement of plant pathogens into new areas cannot be totally controlled.

Conflicts in the Bioherbicidal Approach

In view of the severe limitation placed on the use of exotic microorganisms, much of the work on weed control with plant pathogens is now concentrated on the use of endemic pathogens as bioherbicides. Both the augmentative and inundative approaches (Tisdell *et al.* 1984) are being used. The former is used primarily in areas where long range control is acceptable, such as rangeland and certain aquatic environments, while the latter is used where quick control is desirable, such as in annual crops. Both approaches use essentially the same methodology, differing only in intensity and frequency of pathogen application. Pathogens are grown in artificial culture, harvested and applied to the target plant at an optimal time for infection to occur. This approach has been very successful and two bioherbicides are already being marketed and others may be nearing the marketing stage.

Fungi make up the majority of the pathogen species used in biocontrol programs (Freeman 1980; Templeton *et al.* 1979, 1982). Those that have been used in the bioherbicidal approach are most frequently facultative parasites or, at best, facultative saprophytes. Therefore, they may not be as restrictive in their host range as are the obligate parasites that have been most often used in the classical approach. In fact, many weed-infecting pathogens, such as *Rhizoctonia* spp. (Freeman and Zettler 1971), *Sclerotium rolfsii* (Sacc.) Curzi (Hyphomycetes) (Charudattan 1973) and *Sclerotinia sclerotiorum* (Lih.) de Bary (Helotiales) (Brosten and Sands 1984) have extremely wide host ranges and could be used only under the most restrictive of conditions without causing serious conflicts. Others, including some of the more successful ones such as *Collectotrichum gloeosporioides* (Penz.) f. sp. *aeschynomene* (Melanconiales) (Templeton *et al.* 1978) marketed as Collego® for jointvetch (*Aeschynomene virginica* [L.] B.S.P.; Papilionaceae) in rice and *Phytophthora citrophthora* (R.E. Sm. & E.H. Sm.) Leonian (Peronosporales) (Ridings *et al.* 1972, 1982) marketed as Devine® for milkweed vine control in citrus are physiologically specialized races of these pathogens. It can be speculated that they probably arose as stable mutants, although recent research indicates that the pathovar of *P. citrophthora* from milkweed vines is actually a pathovar of *P. palmivora* (Butler) Butler (Fiechtenberger *et al.* 1981; Ridings *et al.* 1982). Nevertheless, its origin is probably also mutagenic in nature. Again, there is conjecture as to the origin of *Cercospora rodmanii* Conway (Hyphomycetes) (Conway 1976*a*, *b*), a biocontrol agent for waterhyacinth. It also probably arose as a variant of another *Cercospora* sp., *C. piaropi* Tharp., a species known to occur on waterhyacinth since 1917 (Tharp 1917).

The potential for genetic change affecting host range is present in pathogens used as bioherbicides. Certainly, the staggering numbers of propagules used in bioherbicidal applications increase the potential for mutants to occur. For example, *C. gloeosporioides* f. sp. *aeschynomene* has been applied at rates exceeding 150 billion propagules/ha (Templeton *et al.* 1978) and *C. rodmanii* was used at a rate of 40 billion propagules/ha in large-scale tests conducted by the United States Army Corps of Engineers in Louisiana (Theriot and Sanders 1980). Using such numbers certainly increases the possibility of disseminating a mutant with changed host range, although it is not certain that the mutant will survive and multiply. As Leonard (1982) has pointed out, changes in pathogenicity and host-specificity have occurred in certain species of plant pathogens, but experience indicates that such occurrences are rare.

Despite the potential dangers, in the United States the use of bioherbicides has been encouraged by a relaxation in the Environmental Protection Agency (EPA) guidelines for registration of biorational pesticides (Charudattan 1982). The prevailing EPA opinion is that biorational pesticides provide a safer alternative to the use of chemicals in the total environment. However, it should be noted that in view of recent court decisions, this relaxation probably will not apply to genetically engineered organisms should they be forthcoming. This is a serious conflict because of the great potential for tailoring an organism for biocontrol purposes through genetic engineering or mutations (Freeman and Charudattan 1981; Te Beest 1984). Apparently the curent view is that organisms selected through natural mutations are acceptable, but genetically engineered ones are not.

Few, if any, plant pathogens have ever been definitely proven to be pathogenic to either man, domestic animals, wildlife or fishes. In fact, in tests conducted in Florida by Conway and Cullen (1978), fish (*Gambusia*) utilized inoculum of *C. rodmanii* as a food source with no ill effects. However, certain fungi are known to cause allergic reactions in some individuals. This could possibly present a problem in the immediate area of inundative releases, but otherwise, the use of plant pathogens as bioherbicides should cause no conflict with human or other animals.

There are economic conflicts to consider. For example, waterhyacinth control with microbial agents is expected, rather unreasonably, to be as effective as chemical herbicides and as cost effective in practice as chemical herbicides to be accepted. Because this may not be the case, Abbott Laboratories have decided against commercialization of *C. rodmanii* as a bioherbicide based on marketing (economic) reasons.

The potential for toxin production by microbial biocontrol agents has discouraged many companies from entering this field. However, with relaxation of EPA registration requirements, several companies have renewed their search for toxins that may be potentially useful as pesticides. So, what used to be a conflict appears to be no longer a conflict.

Specific Conflicts

In addition to conflicts cited above, several other specific conflicts have occurred. Some of these relate to the fact that the weed is closely related to either a crop or an ornamental species. However, there are instances where the weed species *per se* is considered of economic value under some conditions.

Although it is one of the most important weeds in North America, Watson and Harris (1975) cautioned against the use of pathogens to control wild oats (*Avena fatua* L.; Gramineae) because of the close relationship to cultivated oats (*A. sativa* L.) and the commonality of their pathogens. In Louisiana, work on *Alternaria alternantherae* Holcomb & Antonopoules (Hyphomycetes) for control of alligatorweed (*Alternanthera philoxeroides* [Mart.] Griseb.; Amaranthaceae) was halted because of its pathogenicity on ornamental *Alternanthera* spp. (Holcomb 1978). Likewise in Florida, *Acremonium zonatum* (Saw.) Gams (Hyphomycetes) was purged from the list of potential controls for waterhyacinth because of its pathogenicity on ornamental and edible fig (*Ficus* sp.; Moraceae).

Lantana camara L. (Verbenaceae) is a pest in citrus groves in Florida, but it is also widely used in the State as an ornamental and the proposed use of a *Cercospora* sp. for its control met resistance. A similar situation occurred with alligatorweed in Louisiana where the plant is frequently used as a forage species. Biocontrol agents (insects and pathogens) have contributed to a significant reduction in the population of waterhyacinth. However, recently waterhyacinth has been targeted as an ideal candidate for biomass for the production of alternate sources of fuel. It is also being used to purify sewage effluents. Thus, a plant that was at one time considered the eighth worst weed in the world (Holm *et al.* 1977) is now of potential value.

Conclusion

Plant pathogens are suitable candidates as biocontrol agents for weeds. Although their use for this purpose can be generally safe as indicated by our experience (e.g. *P. chondrillina* in Australia and two mycoherbicides in the U.S.), it is not without potential for conflicts. As with any biological system, changes can occur with pathogens. Such changes may drastically alter the expected equilibrium of the ecosystem. The eventual effects on the agro- and natural ecosystem of the release of a plant pathogen as a biocontrol agent for weeds can be only suggested, never predictable with absolute certainty.

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Tactics for Evading Conflicts in the Biological Control of South African Weeds

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Abstract

Most alien plants now regarded as weeds in South African pastures and conservation areas were introduced intentionally because of their useful or attractive attributes. Therefore, any attempts to control these plants must meet with some opposition which may be minimized or nullified by: (1) selecting, for biological control, only those plants that are generally perceived as important or potentially important weeds (*Opuntia aurantiaca*, *Hakea*, *Sesbania*); (2) selecting natural enemies that reduce aggressiveness and spread of weeds without affecting their useful properties (*Acacia* spp., *Prosopis*); (3) developing techniques and justifying the need for chemical protection of alien plants, where they are useful, as if they were cultivated crops (*Opuntia ficus-indica*); and (4) by encouraging management practices that treat the cause of the problem and not the weed. Exploiting useful attributes of weeds may not necessarily evade conflicts in biological control of alien plants.

Comment Éviter les Controverses en Matière de Lutte Biologique Contre les Plantes Nuisibles en Afrique du Sud

En Afrique du Sud, la majorité des plantes exotiques qui constituent actuellement des plantes nuisibles des pâturages et des réserves naturelles ont été introduites intentionnellement pour leur utilité ou leur attrait. Par conséquent, toute tentative de lutte contre ces plantes suscite nécessairement une certaine opposition qui peut être minimisée ou éliminée: (a) choisir comme candidats pour la lutte biologique uniquement les plantes nuisibles universellement reconnues comme etant trés répandues ou pouvant l'être (*Opuntia aurantiaca*, *Hakea*, *Sesbania*); (b) sélectionner des ennemis naturels qui permettent de réduire le dynamisme et l'extension des plantes nuisibles sans nuire à leurs propriétés utiles (*Acacia* spp., *Prosopis*); (c) encourager l'exploitatoin des plantes nuisibles de manière à en réduire les caractéristiques negatifs (*Acacia longifolia*); (d) mettre au point des techniques visant la protection chimique des plantes exotiques utiles, comme s'il s'aggisait de cultures et justifier pourquoi il faut les protéger (*Opuntia ficus-indica*); et (e) préconiser la mise en oeuvre de techniques de gestion axées sur la source du problème et non pas sur la plante nuisible elle-même.

Introduction

Most introduced plant species that have achieved weed status in South African pastures and in natural vegetation were brought in intentionally during the last two centuries because of their useful or attractive attributes (Shaughnessy 1980). They were nurtured and actively distributed by the early settlers. For instance, annual prizes were awarded for the best patches of Australian acacias cultivated by growers near Cape Town, and foresters were encouraged to fill their saddle bags with seeds of various plants to broadcast during their journeys through the Cape mountains. The aim was to 'afforest' the mountains, which, in spite of their species-rich and unique flora, appeared bare or barren to the early European settlers. As a result of these policies, dense thickets of alien plants now threaten many indigenous and endemic plants in South Africa.

Several species of plants that have become weeds were introduced and cultivated as ornamentals (e.g. *Lantana camara* L., Verbenaceae; *Sesbania punicea* [Cav.] Benth., Fabaceae) or as protective hedges (*Opuntia* spp.; Cactaceae); or as a source of fruit and fodder (*O. ficus-indica* [L.] Miller; *Prosopis* spp., Fabaceae); as a means of consolidating and binding sand-dunes (*Acacia cyclops* A. Cunn. ex G. Don, Fabaceae); as quick-growing firewood (*Hakea sericea* Schrad., *H. gibbosa* [Sm.] Cav., Proteaceae); as shelter and shade plants in the arid interior (*Prosopis* spp.); or as nurse plants (*A. melanoxylon* R. Br.) to provide shade in bare patches of indigenous forests to encourage regeneration of the original hardwood species. For more than a century, the Australian plant *Acacia mearnsii* De Wild. has been grown in large plantations in South Africa as a source of tanning bark and, more recently, as the basis of a wood-chip industry, generating revenue in excess of $40 million/yr. *A. mearnsii* is now one of the worst invasive plants in high-rainfall areas and along streambanks in dry areas, where the species often totally replaces the natural vegetation.

Because of the useful or attractive properties of many of these alien invasive plants, any attempts at biological control must be expected to meet with some opposition and to engender conflicts of interest. In this paper we discuss tactics for evading conflicts of interest in the biological control of South African weeds, including: (1) selection of the target weed species for biological control based on the importance of the plant and on public awareness and support for biological control; (2) selection of agents that reduce seeding and spread of the weeds without jeopardizing their beneficial attributes; (3) the development of methods to protect the plants against introduced natural enemies, where this is beneficial; and (4) suggestions for the treatment of the cause of the weed and not necessarily the weed itself, thus eliminating these species as candidates for biological control. We also discuss exploitation of the weeds as a possible tactic for reducing conflicts of interest, but suggest that this may be unsatisfactory to conservationists whose main concern is the displacement of native vegetation by alien species.

Selecting the Target Weed

There is no potential conflict in mounting a biological control campaign against an invasive plant such as *Opuntia aurantiaca* Lindl. that seemingly has no uses and that is unanimously perceived as an important weed of pastures in South Africa. Usually, however, the biological control practitioner has to decide on priorities for biological control among several weed species of approximately equal importance, each with one or more beneficial properties. A prudent tactic to minimize conflicts in this situation is to select target weeds for biological control that have been identified as problem plants by conservationists, who have themselves mounted campaigns to ensure that the weed is perceived, by the public at large, as a major problem or as a threat (Stirton 1978).

H. sericea is an Australian plant, useful for firewood, that has invaded the Cape mountain vegetation. An extensive educational and awareness campaign by Cape Province conservationists cleared the way for biological control (Neser and Kluge 1985) which then proceeded without opposition.

S. punicea is an attractive garden shrub that has a wide distribution in South Africa but occupies a small area and is of no economic importance. It has proved itself to be a successful competitor and has the potential to expand its range and become an important weed. Except for the rational desire by biological control workers to combat the problem at an early stage, the incentive and motivation for biological control appears to be weak and was not supported until conservationists mounted a 'smear' campaign publicizing the toxic properties of the plant, although no case of poisoning can be attributed directly to this species. Recent initiatives in the biological control of *S. punicea* (Harris and Hoffman 1985) consequently met with no opposition.

Selecting the Agent

A second tactic is to select natural enemies that reduce the aggressiveness and spread of the weeds without affecting their useful properties. Biocontrol of the Australian plant *A. mearnsii* (black wattle) provides an example of this strategy. Because this plant is both an important weed and is widely cultivated for tanning bark and wood, South African entomologists have concentrated their exploratory efforts in Australia on seed-attacking insects, or those that prevent seeding. Growers of black wattle have been gradually persuaded that seed-destroying insects pose no threat to their livelihood and have now largely accepted that carefully screened insects or diseases attacking one *Acacia* species are most unlikely to affect other acacias. Since 1974 when the introduction of any insects against any of the weed acacias was completely unacceptable to the Wattle Growers Institute (Stubbings 1977), biological control using seed-attacking insects has become accepted and the gall wasp, *Trichilogaster acaciaelongifoliae* Froggatt (Hymenoptera: Pteromalidae), that attacks the flower buds of *A. longifolia*, was released in 1981 with most promising results (Neser 1985). Also, specificity testing is near completion on a group of weevils and on other insect species that develop, in Australia, in the green seeds of *Acacia* species. Equally promising is an eriophyid mite that causes 'witch's broom' on the dune-binding weed *Acacia saligna* (Labill.) Wendl. and seems to prevent flowering altogether without killing the plants.

The prospects also seem good for the biological control of *Prosopis glandulosa* Torrey and *P. velutina* Wooten using the seed-destroying bruchid *Algarobius prosopis* (Le Conte) (Coleoptera: Bruchidae). *Prosopis* species provide valuable shelter, and the pods are used as fodder for stock in the dry interior of the country. The plants, however, form dense, impenetrable thickets along dry watercourses and on flood plains; the problem is exacerbated by the rapid spread of the weed after ingestion of the seeds by wild animals, especially porcupines. The bruchids have the potential of reducing seed viability and spread of the plants without harming the trees or preventing use of the pods as fodder.

The fact that seed-attacking insects have been outstandingly successful in regulating weed populations and in reducing the density of these woody invasive plants is illustrated in the report on *Erytenna consputa* Pascoe (Coleoptera: Bruchidae) against *H. sericea* (Neser and Kluge 1985).

Protecting the Plant

Specially selected spineless cultivars of the cactus, *O. ficus-indica*, are commonly planted in dry parts of the country as emergency fodder for stock during droughts. Animals and man spread the seeds of the spineless varieties which segregate back to the prickly variety of *O. ficus-indica* that is still a problem weed in some parts of the country. *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) and *Dactylopius opuntiae* (Cockerell) (Homoptera: Dactylopiidae) originally introduced for the control of *O. ficus-indica* are equally damaging on the spineless varieties. Furthermore, all insects imported for the biological control of cacti in South Africa pose a threat to the planted spineless varieties. In this case, conflicts with farmers who cultivate spineless cultivars have been averted by research and consequent recommendations for techniques that allow them to protect their plants using properly timed applications of insecticides (Burger 1972). The principle has now been accepted that beneficial or ornamental cacti in South Africa should be protected from introduced biological control agents, as if they were crops. As a result, importation and release of insects and pathogens against major cactus weeds such as *O. aurantiaca* in South Africa will not be delayed or prevented by conflicts of interest.

The Wattle Research Institute, representing growers of *A. mearnsii* in South Africa, uses seeds of selected mother plants that have desirable attributes for propagation, and select improved cultivars from wild black wattle populations. They have accepted the need to protect the selected mother trees and the seed orchards against imported seed-destroying insects, and are implementing the use of vegetative reproduction and the cloning of superior plants. This suggests the possibility of cloning sterile cultivars, and vegetative reproduction, as methods for conserving other acacias that are useful in some situations, but which are targets for biological control using seed-attacking insects; e.g. *A. melanoxylon* which is a source of timber, and *A. cyclops* which is used for shelter and for windbreaks.

Treating the Cause

Many weeds of pastures or rangelands, whether they are alien or native species, are symptoms of over-exploitation or poor management. Various thistle species in South Africa, for example, focus attention on the basic causes of the problem and act as caretaker plants because they are unpalatable to stock and survive to protect the topsoil from erosion. Thistles should therefore remain low on the priority list for biocontrol, except for seed-attacking insects that may be useful in preventing the spread of the plants. Responsibility for remedial treatment of the cause of the thistle problem should be shifted to pasture scientists.

A parallel case is that of the water hyacinth (*Eichhornia crassipes* [Mart.] Solms-Laubach (Pontederiaceae) which in most situations where it is a weed in South Africa, is a symptom of eutrophication and mineralization of the water. Water hyacinth grew so densely on Hartbeespoort Dam, for example, that yachts were unable to move on the water. Herbicides were used to kill the plants but subsequent growth of algae and other water plants in the enriched medium produced highly odorous water, with a colour and consistency of thick pea soup, so thick in places that birds were able to run on the 'water' surface. Residents around the perimeter of the lake were understandably angry. Biocontrollers may have been included in the acrimony had the early decision not been taken to move away from the biological control of water hyacinth, and to encourage the view that the weed was a symptom of pollution that would not be rectified even if biological control were successful.

Many potential conflicts of interest could also be avoided by accepting that the cause of the problem may be the ill-considered importation of alien plants for functions that could be performed as well or better by indigenous South African plants, for example the use of native plants for hedges or as screen plants, and the use of indigenous plants rather than aliens for stabilizing sand-dunes.

Exploiting the Weed

Cynically, a weed may be defined as a plant for which a use has not been found. On this basis, maximum exploitation of weeds, for instance *A. longifolia* as firewood and fodder, *O. ficus-indica* as a source of fruit or as a salad vegetable, and as a substrate for the carmine-producing cochineal insect, *Dactylopius coccus* O. Costa, should be encouraged as an expedient to reduce the problem status of the plants and to avoid the difficult issue of whether or not a biological control programme should be mounted. Superficially, this expedient seems sensible and economically viable but it is not necessarily acceptable to conservationists, and others, if the alien plants displace indigenous vegetation. Thus, encouraging the exploitation of some alien plants may create conflicts where none previously existed, so this tactic, perhaps, cannot be regarded as a legitimate policy for evading conflicts in the biological control of weeds.

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Native Plant Considerations in the Biological Control of Leafy Spurge

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Abstract

In North America leafy spurge is a complex of forms, species, and hybrids which has most frequently been called *Euphorbia esula*. Leafy spurge is a deep-rooted perennial weed that is primarily a problem in the Great Plains region of the U.S. and Canada because it is toxic to some classes of livestock and displaces more desirable forage plants. Biological control research, which was begun in the early 1960s, has yet to produce insects which cause a reduction in the plants, but still holds promise. A significant consideration with the biological control effort on leafy spurge is the presence of 107 native *Euphorbia* and four or five native *Chamaesyce* species which could be used and damged by the agents introduced for leafy spurge control. Almost one-third of these native spurges are sympatric with leafy spurge. Although these natives have no known economic value, 11 are rare and under review for Federal protection as threatened or endangered species. Even though *Euphorbia purpurea*, in the mideastern U.S. is the only rare species under review which is sympatric with leafy spurges, other rare spurges could also be attacked. This is based on the large number (25) of spurges that are sympatric with both leafy spurge and the rare spurges which could serve as bridges to carry the biological agents from leafy spurge to the rare species. Just what the actual levels of risks are, or what damage to or even elimination of some native spurges would mean are complex issues, relating not only to the scientific possibilities and effects, but also to the various interests and values of our country. To what extent the use of native spurges would occur depends primarily upon the host plant specificity levels (within the genus *Euphorbia*) of the agents involved since most of the insects have relatively broad climatic tolerances. There are large differences in the host plant specificity levels of the leafy spurge insects, although not much is known about this for the insects utilized earlier in the program (*Hyles euphorbia* and *Oberea erythrocephala*). The current strategy is to select among the newer candidates, and the other as yet unknown organisms, species which are broad enough in their host ranges to accept the diverse forms of leafy spurge and yet narrow enough to exclude the use of most native spurges, and the rare species under review in particular. While the leaf-tier, *Lobesia euphorbiana*, seems likely to be able to use most native spurges, it appears that *Aphthona flava*, a root-borer, and *Bayeria capitigena*, a shoot gall midge, with host plant specificity levels below the subgenus Esula level, do meet these criteria. These two insects may help us to begin to reduce the abundance of leafy spurge while remaining attentive to the native spurge considerations.

Considerations en ce qui Concerne les Plantes Indigènes en Matière de Lutte Biologique Contre l'Euphorbe Touffue

En Amérique du Nord l'euphorbe touffue 'leafy spurge' constitue un complexe de formes, d'espèces et d'hybrides qu'on cite, le plus souvent, sous le non *Euphorbia esula*. L'euphorbe touffue est une mauvaise herbe vivace à racine longue, qui donne des problèmes principalement dans la région des grandes plaines des États-Unis et du Canada, à cause de sa toxicité pour certains espèces de bêtail et parce qu'elle chasse des fourrages plus désirables. La recherche en matière de lutte biologique a commencée peu après 1960, et, quoique n'ayant pas produit, jusqu'ici, d'insectes capables de tenir en échec les plantes nuisibles, elle promet encore des résultats. La presence de 107 espèces indigènes d'*Euphorbia* et de 4 ou 5 de *Chamaesyce* qui pourraient être utilisées et endommagées par les agents introduits pour contrôler l'euphorbe touffue est une considération significative pour cette recherche. A peu près le tiers de ces euphorbes indigènes sont sympatriques avec l'euphorbe touffue. Si ces espèces indigènes n'ont aucun valeur économique, à notre connaissance, onze d'entre elles sont rares, menacées peut-etre, et leur protection, au niveau fédéral est actuellement envisagée. Même si au centre-est des États-Unis, l'*Euphorbia purpurea* soit la seule espèce rare et sympatrique avec l'euphorbe touffue, dont la protection est envisagée, il pourrait exister d'autres espèces rares et susceptibles d'être attaquées. Ceci se base sur le nombre éléve (25) d'euphorbes qui sont sympatriques tant avec l'euphorbe touffue, qu'avec les espèces rares et qui pourraient se servir de 'ponts' pour transferer les agents biologiques de l'euphorbe touffue aux espèces rares. Quelles sont précisément l'importance réalle des risques et les implications de l'endommagement, voire l'élimination de quelques euphorbes indigènes, sont des questions complexes qui sont liées non seulement aux possibilités et effets scientifiques, mais aussi aux divers interêts et valeurs de notre pays. La mesure dans laquelle des euphorbes indigènes seraient utilisées depend en premier lieu des spécificités vis-à-vis les plantes-hôtes (du genre *Euphorbia*) des agents choisis, puisque la plupart de ces insectes ont des tolérances climatiques assez larges. Il y a de grandes différences de spécificité vis-à-vis les plantes-hôtes chez les insectes de l'euphorbe touffue, mais on sait peu à ce sujet en ce qui concerne les insectes (*Hyles euphorbia* et *Oberea erythrocephala*) utilisés précédemment dans la programme de recherche. La stratégie actuelle est de trier parmi les candidats plus récents, ainsi que d'autres organismes encore inconnus, des espèces dont l'éventail des hôtes est assez large pour qu'elles acceptent les formes diverses de l'euphorbe touffue, mais en même temps assez restreint pour exclure la plurpart des euphorbes indigènes, et en particulier, les espèces rares dont la protection est envisagée. Si *Lobesia euphorbiana* (lieur de feuilles) paraît pouvoir utiliser la plupart des euphorbes indigènes, *Apthona flava* (rongeur des racines) et *Bayeria captigena* (mouche, faisant des galles aux pousses), dont les spécificités sont en-dessus du niveau du sous-genre *Esula*, semblent satisfaire à nos critères. Ces deux insectes pourraient nous aider à réduire l'abondance de l'euphorbe toufue, tout en ayant à l'esprit les considérations concernant les euphorbes indigènes.

Introduction

In North America, leafy spurge is a complex of forms, species, and hybrids which has most frequently been called *Euphorbia esula* L. (Euphorbiaceae). The most common problem type appears to be *E.* × *pseudovirgata* which is a hybrid of *E. esula sensu stricto* and *E. waldsteinii* (= *E. virgata* Waldst. & Kit.) (Dunn and Radcliffe-Smith 1980). *E. esula*'s range in its native Eurasia is from Spain and Portugal (Radcliffe-Smith and Tutin 1968) to China (Steward 1958) and Japan (Ohwi 1965). *E. waldsteinii* (as *E. virgata*) is native to central and eastern Europe (Radcliffe-Smith and Tutin 1968). The taxonomy of this leafy spurge complex is not yet resolved and is under study by a number of workers.

Leafy spurge (Fig. 1) is a perennial herb with a deep and extensive root system. The plants reproduce vegetatively to form persistent patches which coalesce to form large stands. Spread is by seed, which can be ejected as far as 5 m from their explosive capsules (Bakke 1936). Animals, water, and human activities are thought to serve to disperse the seed (Selleck *et al.* 1962). This spurge has very broad ecological tolerances (Selleck *et al.* 1962).

Leafy spurge was first recorded in the U.S. at Newburry, Massachusetts, in 1827 (Britton 1921) but probably has had many separate introductions (Dunn 1979). Its distribution in the U.S. (as of 1979) is shown in Fig. 2 (Dunn 1979). The main problems caused by leafy spurge are toxicity to some classes of livestock, and reduction of desirable forage plants, which occurs through competition (Selleck 1959) and selective grazing by cattle which usually refuse to eat the plant (Dunn 1979). Peter Harris' (Agric. Can., Regina, Saskatchewan, pers. comm.) examination of the change in the spurge abundance over a 30-yr period in Saskatchewan found that the plant 'disappeared in the course of normal agricultural practices on land broken for cereal production but on permanent grasslands the infested area had approximately doubled in spite of the control program'. The primary control method used against leafy spurge has been with selected herbicides.

A biological control program against this weed was initiated in the early 1960s by Canada in response to its spread and the high costs of chemical control. The first leafy spurge biological control agent, the spurge hawk moth, *Hyles euphorbiae* (L.) (Lepidoptera: Sphingidae), was imported from Europe and released in North America beginning in 1965 (Harris 1984). The U.S. Department of Agriculture joined the effort in the mid-1970s, at first only to utilize insects cleared for introduction by the Canadians, then to develop its own candidate agents. After > 20 yrs since the program was initiated, a number of insect species have been released against leafy spurge (discussed later), but not much progress had been made. Although a large number of insects are restricted to the genus *Euphorbia* in Europe, it has been difficult to find species which will survive and be effective in North America on a leafy spurge which seems to be a complex (Harris 1984). It is probable that a complex of biological control agents exerting an intense level of pressure on the plants will be required for leafy spurge to be reduced, since plants can readily regenerate from their latex-rich root system following destruction of the above-ground stems. When leafy spurge is managed using sheep, the animals need to be continuously pastured with the plants to keep the latter's density low. These factors suggest that even before (or without) the native spurge conflict, that biological control of leafy spurge has been, and is, a difficult task.

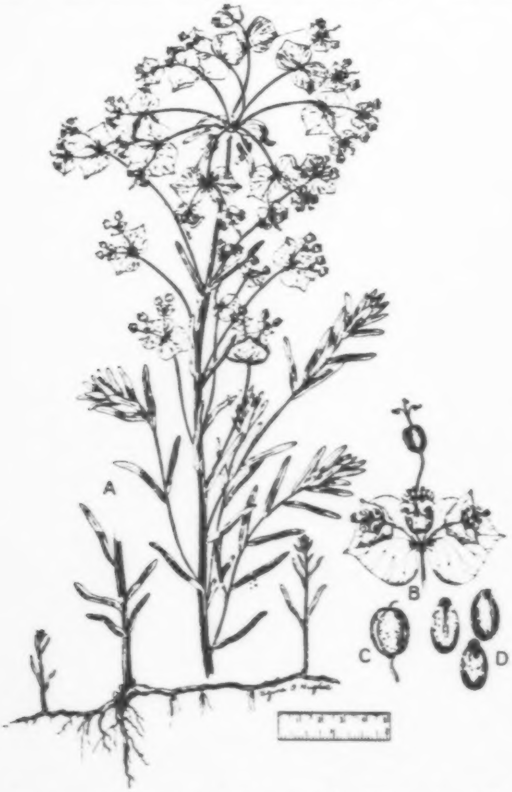

Fig. 1. Leafy spurge (*Euphorbia esula* L. complex) (after Reed and Hughes 1970).

An examination of the native plant issue with the biological control of leafy spurge program was begun for a number of reasons. First was the recognition of the large number of U.S. native spurges (*Euphorbia* and *Chamaesyce* species) that could become non-target hosts for biological control agents introduced against leafy spurge. Secondly, U.S. environmental legislation was passed which regulated the action of the Federal Government agencies in relation to the environment (the National Environmental Policy Act, NEPA, 1969, U.S. Government Council on Environmental Quality, 1978; and the Endangered Species Act, 1973, 1978). Part of the Endangered Species Act was the listing, by the U.S. Fish and Wildlife Service (1980, 1983), of many rare spurges as candidates for legal protection as endangered or threatened species. Finally, detection of movement of insects introduced for biological control of weeds, from the target weeds to their non-target native relatives, in four of the USDA's past projects: from *Silybum marianum* (L.) Gaertn. and *Carduus* spp. to *Cirsium* spp. (all Asteraceae) (Turner, Pemberton, and Rosenthal, unpubl. data); from *Tribulus terrestris* L. to *Kallstroemia* spp. (both Zygophyllaceae) (Hawkes and Turner, unpubl. data); from *Hypericum* *perforatum* L. to *Hypericum* spp. (Clusiaceae) (Andres 1985); and from *Alternanthera philoxeroides* (Mart.) Griseb. to *Philoxerus vermicularis* (L.) R. Br. ex J.E. Smith (both Amaranthaceae) (Vogt, USDA, Stoneville, Miss., unpubl. data). Although the effects of these movements are unknown, they are not necessarily significant. However when coupled with the above-mentioned legislation plus the large numbers of native spurges that occur in North America, an analysis of the potential use of these plants by candidate agents seemed necessary.

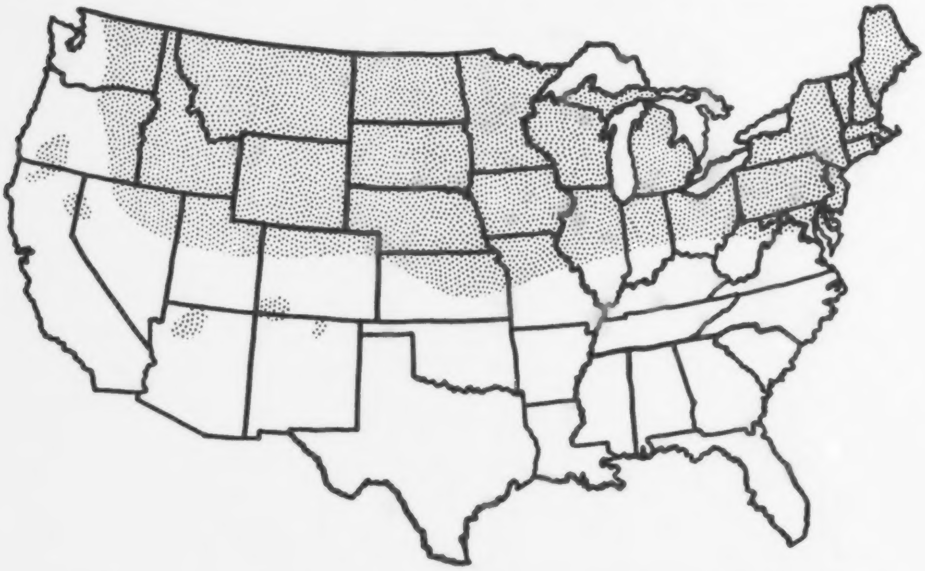

Fig. 2. The distribution of leafy spurge in the United States as of 1979 (modified from Dunn 1979).

To understand the nature of the biological control of leafy spurge–native plant issue, I examined the numerous plant species, their diverse taxonomic affinities, geographic distributions, and other characteristics which relate to their potential use by biological control agents. The native spurges which are used in the host plant specificity testing are then discussed. This will be followed by a description of the principal leafy spurge insects, their known host plant specificity levels, and current status in the project. After this, a discussion of the potential risks of use and harm to native spurges, and the meaning and implications of this use will be made. In conclusion are some comments on the strategy and prognosis in dealing with this leafy spurge–native spurge issue.

The Plants

Table 1 lists the spurges which occur in America north of Mexico. There are 111–112 native spurges (107 *Euphorbia* spp. and 4–5 native *Chamaesyce* spp.) and 13 introduced *Euphorbia* spp. *Chamaesyce* and *Euphorbia* are closely related genera in the Euphorbiaceae. The subgenus Chamaesyce, within the genus *Euphorbia*, frequently has had many or all of its species placed in the genus *Chamaesyce* and vice versa. Insects which have 'genus' level host specificity breadths usually feed on both *Chamaesyce* and *Euphorbia* spp. The subgenus for each of the spurge species is listed in Table 1. The subgeneric concept is not only a very useful way of dealing with the large number of *Euphorbia* spp., but also appears to provide quite 'natural' groupings which reflect true phylogenies (M. Huft, Field Museum, Chicago, pers. comm.). Many *Euphorbia*-feeding insects respond to these subgenera, accepting as host plants most of the species in one or more of the subgenera and rejecting the species in other subgenera.

In North America, there are four subgenera including Esula with 21 spp., Agaloma with 26 spp., Poinsettia with 3 spp., and Chamaesyce with 57 spp. (This information and much of that relating to the characteristics of spurges was compiled from the references listed in the literature cited section and marked with an asterisk.) In Europe all but 4 of the 105 *Euphorbia* spp., which are subgenus Chamaesyce spp., belong to the subgenus Esula (Radcliffe-Smith and Tutin 1968). Leafy spurge belongs to the subgenus Esula. North American euphorbias which belong to this subgenus are then the most closely related species to leafy spurge and thus presumably the most subject (by taxonomic affinity) to use by agents introduced for leafy spurge control. All of the European host plant records for *Euphorbia*-feeding insects are from subgenus Esula spp. and therefore provide no indication whether North American Poinsettia, Agaloma or Chamaesyce spurges could become hosts for these insects.

Table 1 also provides distribution codes for each spurge species. Each code represents the occurrence of the plant in a particular region, as shown on the accompanying Soil Conservation Service map (Fig. 3). The next column in Table 1 indicates whether a particular spurge is sympatric with leafy spurge. These are the plant species that, depending on the level of host plant specificity for a particular agent, would be most likely to become host plants for leafy spurge biological control agents. In all, 32 and possibly as many as 41 native spurges have overlapping ranges with leafy spurge. Table 2 summarizes the numbers of spurges, their subgenera, habits, sympatric species with leafy spurge, rare review species, etc.

Table 1 also indicates whether a particular spurge is a rare species under review for Federal protection as a threatened or endangered species. Table 3 treats these rare review species a little more fully, giving more specific information about life form, habitat, location, and review category. Currently there are nine *Euphorbia* and two *Chamaesyce* spp. under review. Fig. 4 indicates the approximate location of these species. Most of these rare spurges are habitat specialists. Only one of these species, *E. purpurea* (Raf.) Ferald, which occurs in the mideastern U.S. is sympatric with leafy spurge. This species is a robust perennial which belongs to the subgenus Esula, qualities that could increase the risk of its use by spurge-feeding insects.

The possibility that other rare and endangered *Euphorbia* and *Chamaesyce* spp. could be used by insects introduced for leafy spurge control is still significant, even though there is no overlap in the distributions of these plants and leafy spurge. This is based

Table 1. ***Euphorbia* and *Chamaesyce* species which occur in America North of Mexico[1].**

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protection	Potential bridge leafy spurge to a species under review
E. abramsiana L.C. Wheeler	Annual	chamaesyce	7 0			
E. acuta Engelm.	Perenn.	agaloma	6 7			
E. albomarginata Torr. & Gray	P	chamaesyce	6 7 8 0	possibly		possibly
E. alta J.B.S. Norton	P	esula sec. galarrhoei	7			
E. ammannioides H.B.K.	A	chamaesyce	1 2 6			
E. angusta Engelm.	P	agaloma	6			
E. antisyphilitica Zuccar	P	agaloma	6			
E. arizonica Engelm.	P	chamaesyce	6 7 0			
E. astyla Engelm. ex Boiss.	P	chamaesyce	6			
E. bicolor Engelm. & Gray	A	agaloma	2 6			
E. bifurcata Engelm.	A	agaloma	6 7			
E. bilobata Engelm.	A	agaloma	6 7			
E. blodgettii Engelm. A. Hitchc.	P	chamaesyce	2 0			
E. brachycera Engelm.	P	esula sec. esula	6 7 8	possibly		possibly
E. capitellata Engelm.	P	chamaesyce	7			
E. carunculata Waterfall	A	chamaesyce	6			
E. chamaesula Boiss.	P	esula sec. esula	7			
E. cinerascens Engelm.	P	chamaesyce	6			
E. commutata Engelm.	A	esula sec. esula	1 2 3 5 6 7	possibly		yes
E. conferta (Small) B.E. Smith	A	chamaesyce	2			
E. cordifolia Elliot	A	chamaescye	2 6			
E. corollata L.	P	agaloma	1 2 3 4 5 6 E	yes		yes
E. crenulata Engelm.	A	esula sec. esula	8 9 0	yes		yes
E. curtisii Engelm.	shrub	agaloma	2			
E. cyathophora Murray	A	poinsettia	1 2 3 4 5 6	yes		yes
**E. cyparissias* L.	P	esula sec. esula	1 2 3 4 5 8 9 H W P E M	yes		yes
E. deltoidea Engelm. ex Chapm.	P	chamaesyce	2		yes	
E. dentata Michx.	A	poinsettia	1 2 3 4 5 6	yes		yes

Table 1. Continued.

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protection	Potential bridge leafy spurge to a species under review
			7 H E			
E. discoidalis Chapm.	P	agaloma	2			
E. eriantha Benth.	A	agaloma	6 7 0			
**E. esula* L.	P	esula sec. esula	1 3 4 5 8 9 0 W P E M			
**E. exigua* L.	A	esula sec. esula	1 6 0 W E M	yes		
E. exserta (Small) Coker	P	agaloma	2			
E. exstipulata Engelm.	A	agaloma	6 7			
**E. falcata* L.	A	esula sec. esula	1	yes		
E. fendleri Torr. & Gray	P	chamaesyce	4 5 6 7 8 9 0	yes	yes'	yes
E. florida Engelm.	A	chamaesyce	7			
E. floridana Chapm.	P	esula sec. ipecacuanhe	2			
E. garberi Engelm. ex Chapm.	A	chamaesyce	2		yes	
E. geyeri Engelm.	A	chamaesyce	3 4 5 6 7 P	yes		yes
E. glyptosperma Engelm.	A	chamaesyce	1 3 4 5 6 7 8 9 0	yes		yes
E. golondrina L.W. Wheeler	A	chamaesyce	6		yes	
E. gracillima S. Wats.	A	chamaesyce	7			
**E. helioscopia* L.	A	esula sec. galarrhoei	1 2 3 6 9 0 W P E M	yes		
E. helleri Millsp.	A	esula sec. esula	6			
E. heterophylla L.	A	poinsettia	1 2 3 4 6 7	yes		yes
E. hexagona Nutt. ex Spreng.	A	agaloma	2 3 4 5 6	yes		yes
E. hirta L.	A	chamaesyce	2 6 7			
E. hooveri L.C. Wheeler	A	chamaesyce	0		yes	
E. humistrata Engelm.	A	chamaesyce	1 2 3 5 6	yes		yes
E. hyperifolia L.	A	chamaesyce	2 6			
E. hyssopifolia L.	A	chamaesyce	2 6 7			
E. incisa Engelm.	P	esula sec. esula	7 8 0	possibly		

Table 1. Continued.

Euphorbia or _Chamaesyce_ species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protection	Potential bridge leafy spurge to a species under review
E. indivia (Engelm.) Tidest.	A	chamaesyce	6 7			
E. innocua L.C. Wheeler	P	agaloma	6			
E. inundata Turr. ex Chapm.	P	esula sec. ipecacuanhe	2			
E. ipecacuanhae L.	P	agaloma	1 2	yes		possibly
E. jejuna M. Johst. & Warnock.	P	chamaesyce	6			
E. laredana Millsp.	P	chamaesyce	6			
E. lata Engelm.	P	chamaesyce	5 6 7	yes		possibly
*_E. lathyris_ L.	A	esula sec. esula	1 2 7 9 0 W E	yes		
E. longicruris Scheele	A	esula sec. esula	2 6			
*_E. lucida_ Waldst. & Kit.	A	esula sec. esula	1 3 W P E	yes		
E. lurida Engelm.	P	esula sec. esula	7 8	yes		
E. macropus (Klotzsch & Garcke) Boiss.	P	agaloma	7			
E. maculata L. (=_E. supina_)	A	chamaesyce	1 2 3 4 5 6 7 9 0 E M	yes		yes
E. marginata Pursh	A	agaloma	1 2 3 4 5 6 P E	yes		yes
E. melanadenia Torr.	P	chamaesyce	7 0			
*_E. mendezii_ Boiss.	P	chamaesyce	2			
E. mercurialina Michx.	P	agaloma	1 2	yes		
E. mesembriantemifolia Jacq.	shrub	chamaesyce	2			
E. micromera Boiss.	A	chamaesyce	6 7 8 0	possibly		possibly
E. misera Benth.	shrub	agaloma	0			
E. missurica Raf.	A	chamaesyce	2 3 5 6 7 9	yes		yes
E. nephradenia Barneby	A	agaloma	8	yes		
*_E. nutans_ Lab.	A	chamaesyce	1 2 3 4 5 6 9 0	yes		yes
*_E. oblongata_ Griseb.	A	esula sec. esula	0			
E. obtusata Pursh	A	esula sec. galarrhoei	1 2 3 5 6	yes		yes
E. ocellata E.M. Durand & Hilgard	A	chamaesyce	7 8 0	yes		possibly

Table 1. Continued.

Euphorbia or *Chamaesyce* species (• introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protection	Potential bridge leafy spurge to a species under review
E. ophthalmica Pers.	A	chamaesyce	2			
E. palmeri Engelm.	P	esula sec. esula	7 8 0	possibly		possibly
E. parishii Greene	P	chamaesyce	8 0			
E. parryi Engelm.	A	chamaesyce	6 7 8 0	yes		possibly
E. pediculifera Engelm.	P	chamaesyce	7 0			
E. piplidion Engelm.	A	esula sec. esula	6			
•*E. peplus* L.	A	esula sec. esula	1 2 3 7 9 0 H W P E M	yes		yes
E. perennans (Shinners) Warnock & M. Johnst.	P	chamaesyce	6		yes	
E. pergamena Small	P	chamaescye	2			
•*E. platyphylla* L.	A	esula sec. galarrhoei	1 3 E	yes		
E. platysperma Englem.	A	chamaesyce	0		yes	
E. polycarpa Benth.	P	chamaesyce	7 8 0	possibly		possibly
E. polyonifolia L.	A	chamaesyce	1 2 3 E M	yes		
E. polyphylla Engelm. ex Chapm.	P	agaloma	2			
E. prostrata Ait.	A	chamaesyce	2 5 6 7 0	yes		yes
E. pubentissima Michx.	P	agaloma	1 2	possibly		
E. purpurea (Raf.) Fernald	P	esula section[4]	1 2	yes	yes	
E. pychanthema Englem.	AP	chamaescye	6			
E. radicans Benth.	P	agaloma	6 7			
E. revoluta Englem.	A	chamaesyce	5 6 7 0			
E. robusta (Engelm.) Small	P	esula sec. esula	4 5 7 8 9	yes		yes
E. roemerana Scheele	A	esula sec. esula	6			
•*E. segetalis* L.	A	esula sec. esula	1			
E. serpens H.B.K.	A	chamaesyce	1 2 3 4 5 6 7 8 9 0 E	yes		yes
E. serphyllifolia Pers.	A	chamaesyce	3 4 5 6 7 8 9 0 W P E M	yes		yes
E. serrula Englem.	A	chamaesyce	6 7	possibly		possibly

Table 1. Continued.

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protection	Potential bridge leafy spurge to a species under review
E. setiloba Engelm.	A	chamaesyce	6 7 8 0	possibly		possibly
E. simulans (L.C. Wheeler) Warnock & M. Johnst.	AP	chamaesyce	6			
E. spatulata Lam.	A	esula sec. galarrhoei	2 3 4 5 6 7 8 9 0	yes		yes
E. strictospora Engelm.	A	chamaesyce	3 4 5 6 7	yes		yes
E. strictior Holz	P	agaloma	6 7	possibly		
E. telephiodes Chapm.	P	esula sec. ipecacuanhe	2		yes	
E. tetrapora Engelm.	A	esula sec. esula	2 6			
E. theriaca L.C. Wheeler	A	chamaesyce	6			
E. trachysperma Engelm.	A	chamaesyce	7			
E. trichotoma H.B.K.	P	esula sec. esula	2			
E. vallis-mortae (Millsp.) J.T. Howell	P	chamaesyce	0			
E. vermiculata Raf.	A	chamaesyce	1 3 5 7 W E M	yes		
E. vilifera Scheele	P	chamaesyce	6			
E. wrightii Torr. & Gray	P	agaloma	6			
E. zinniiflora Small	P	agaloma	1 2	yes		
C. cumulicola Raf.	A	--	2		yes	
C. pinetorum Small	P	--	2			
C. porterana Small	P	--	2		yes	
C. serpens[5] (H.B.K.) Small	A	--	2			
C. thymifolia (L.) Millsp.	A	--	2			

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[1] Based upon "National list of scientific plant names", Soil Conservation Service, authored by M. Huft. Field Museum of Natural History, Chicago.

[2] See the Soil Conservation Service map (Fig. 3) for the location of the distribution codes.

[3] Only *Europhorbia fendleri* : var. triligulata is undr review, other subspecific taxa of *E. fendleri* are not being reviewed.

[4] *E. purpurea* not placed in a section by Norton (1900).

[5] Area of origin uncertain.

on the large number of other spurge species which could serve as bridges to carry biological control agents from leafy spurge to the endangered spurges. For a spurge species to be a bridge, it must be first an acceptable host to a particular natural enemy, and then be sympatric with both leafy spurge and an endangered spurge. Table 1 identifies at least 25 spurge species which could become bridges. It is also possible, but more difficult, for natural enemies to move from leafy spurge to a species under review through a series of other spurge species, which individually could not bridge the total distance between them.

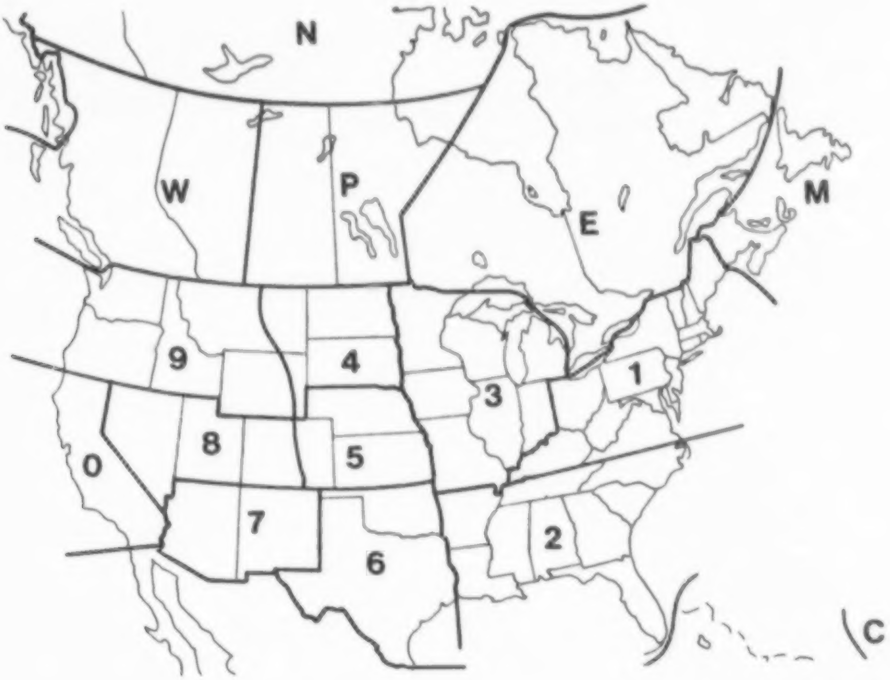

Fig. 3. Regional distribution codes for the spurge species listed in Table 1 (from U.S. Department of Agriculture 1982).

To what extent this bridging would occur depends primarily upon the host plant ranges of the biological control agents used. Leafy spurge's natural enemies, which have genus-level host specificity levels, could in theory use all 25 spurge bridges to move onto the 11 rare species under review. Agents which are restricted to using species of the subgenus Esula (the leafy spurge group) would have four potential bridges to *Euphorbia telephiodes* Chapm. This spurge is one of two subgenus Esula spp. under review, *E. purpurea* which is sympatric with leafy spurge is the other. Fig. 5 shows the distribution of *E. spatulata* Lam., a widespread subgenus Esula species which is a potential bridge. Figs. 6 and 7 show, respectively, the ranges of *E. maculata* L., a subgenus Chamaesyce potential bridge, and *E. marginata* Pursh, a subgenus Agaloma potential bridge. When these maps are compared with the map of leafy spurge (Fig. 2) and the map showing the occurrence of the spurges under review (Fig. 4), the potential for bridging can be seen.

The degree of use of native non-target spurges by leafy spurge biological control agents should be directly related to the breadth of their host ranges, which at this point is imperfectly known.

Table 2. North American spurges (*Europrbia* and *Chamaesyce*) summary list.

Euphorbia	
1. Number of *Euphorbia* species	120
2. Number of introduced *Euphorbia* species	13
3. Number of native *Euphorbia* species (50 perennials and 57 annuals)	107
4. Number of native *Euphorbia* species in the subgenus esula (12 perennials and 9 annuals)	21
5. Number of native *Euphorbia* species in the subgenus agaloma (14 perennials and 8 annuals)	26
6. Number of native *Euphorbia* species in the subgenus poinsettia (all perennials)	3
7. Number of native *Euphorbia* species in the subgenus chamaesyce (21 perennials and 36 annuals)	57
8. Number of native *Euphorbia* species sympatric with leafy spurge (7 esulas, 7 agalomas, 3 poinsettias and 15 chamaesyces) (9 other species may be sympatric with leafy spurge)	32
9. Number of rare *Euphorbia* species under review for legal protection as endangered or threatened species (variety triligulata of *E. fendleri* under review is included, other subtaxa of this species are not rare)	9
10. Number of potential species bridges that could carry introduced biological control agents from leafy spurge to rare *Euporbia* species under review (7 esulas, 4 agalomas, 3 poinsettias and 11 chamaesyces) (11 additional species may be potential bridges)	25
Chamaesyce	
1. Number of *Chamaesyce* species (2 perinnials and 3 annuals)	5
2. Number of native *Chamaesyce* species (the origin of *E. mendezii is uncertain)*	4-5
3. Number of *Chamaesyce* species which are sympatric with leafy spurge or which could serve as bridges to rare species	0
4. Number of rare *Chamaesyce* species under review for endangered or threatened status	2
Totals	
Combined total of native spurge species (*Euporbia* and *Chamaesyce) in* America north of Mexico	111-112
Total number of rare spurges under review for legal protection	11

Table 4 lists the native *Euphorbia* spp. used in host specificity testing at the USDA's Albany quarantine. The purpose of the Albany program is to try to predict what the potential host range, within the North American *Euphorbia*, could become if a particular organism was introduced. When a candidate insect comes to Albany, it has been determined to be specific to the genus *Euphorbia* by the overseas testing programs in Rome, Italy, Delemont, Switzerland, or Regina, Canada. Usually few native North American spurges have been tested. The test plants at Albany are selected to represent the four different subgenera (Agaloma, Chamaesyce, Esula, and Poinsettia) of the genus *Euphorbia* which occur in North America. Most of the species (10 or 12) are sympatric

Table 3. Rare spurges under review for legal protection as endangered or threatened species[1].

Species	Subgenus	Habit and Size	Habitat	Locality	Review Catagory[2]	Comments
1. *Chamaesyce cumulicola* Raf. (= *Euphorbia cumulicola*)	Chamaesyce of Euphorbia	prostrate or decumbent annual herb	Coastal dunes and scrub	Cape Romano region and lower southeastern coast of So. Fla.	2	
2. *C. porterana* Small (= *Euphorbia porterana*)	Chamaesyce of Euphorbia	erect or ascending perennial herbs 3-10 cm tall	Pinelands and coast scrub	Dade and Monroe Co. and the Keys of So. Fla.	1	probably will be proposed[3]
C.p. var. *keyensis*	"	"	Coastal scrub on limestone soils and sandy areas	Florida Keys	1	"
C.p. var. *porterana*	"	"	Pinelands on limestone soils	Dade & Monroe Co., Fla	1	"
C.p. var. *scaparia*	"	"	Pinelands on limestone soils	lower Fla. Keys	1	"
3. *Europhorbia deltoidea* Engelm. ex Chapm	Chamaesyce	prostrate perennial herbs forming dense mats	Pinelands	Dade Co. and Keys of Fla.	1	probably will be proposed[4]
E.d. spp. *deltoidea*	"	"	"	Dade Co. Fla.	1	"
E.d. spp. *serpyllum*	"	"	"	Lower Fla. Keys	1	"
4. *E. fenderli* Torr. & Gray var. *triligulata*	Chamaesyce	decumbent to erect perennial herb 5-15 cm long	—	Big Bend area of Texas	2	other subtaxa of E. *fenderli* are not rare

Table 3. Continued.

Species	Subgenus	Habit and Size	Habitat	Locality	Review Catagory[2]	Comments
5. *E. garberi* Engelm. ex Chapm.	Chamaesyce	robust prostrate or low ascending robusta annual herb to 3 dm long.	Pinelands and hamocks	Florida	1	
6. *E. golondrina* L.W. Wheeler	Chamaesyce	prostrate annual herb 5-35 cm long	Alluvial or eolian soils	Deserts of So. Brewster Co., Tex.	2	
7. *E. hooveri* L.C. Wheeler	Chamaesyce	prostrate or decumbent annual herb 5-20 cm long	Dried mud flats and dried vernal pools in Valley Grassland Community	Near Vina in Tehama Co. and Visalia in Tulare Co., Calif.	1	probably will be proposed[5]
8. *E. perennans* (Shinners) Warnock & M. Johnst.	Chamaesyce	perennial herb 13-47 cm tall with 5-20 erect stems and woody tap root	Gypsum soils	Terlingua-Lajitas areas of S.W. Brewster Co., Texas	2	
9. *E. platysperma* Engelm.	Chamaesyce	prostrate annual 1-2.5 cm long	Sandy soil in in the Creosote Bush Community	Near Thousand Palms in Coachella Valley, Calif. and the Yuma area of Calif. and Ariz.	2	
10. *E. purpurea* (Raf.) Fernald	Esula	perennial herb to	Dry but more frequently moist	Carroll Co., Maryl.; Ashe, Buncombe,	2	No action planned at

Table 3. Continued.

Species	Subgenus	Habit and Size	Habitat	Locality	Review Catagory[2]	Comments
		1 m tall growing from a short stout woody rhizome	or swampy woods and thickets	Haywood, Jackson, Macon, Mitchell and Watauga Co., N.C.; Rockbridge Co., Vir.; Pocahontas, Preston, Randolph and Tucker Co., W. Vir.	2	present[6]
11. *E. telephiodes* Chapm.	Esula	robust perennial herb to .3 m	Dry sandy pine palmetto savannas	Near the Apalachicola river in Franklin Co. and Port St. Joe in Gulf Co. of panhandle, Fla.	2	Abundant within its very limited habitat[7]

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[1] Based upon the 1980 U.S. Fish and Wildlife listing which was amended in 1983.

[2] Review categories for listed taxa were defined and assigned in the 1980 and 1983 listings. Catagory 1 indicates that sufficient information is on hand to support the biological appropriateness for the listing of a species to be listed as Endangered or Threatened.

[3] Andy Robinson, Botanist, Office of Endangered Species (FWS), Reg. 1, Portland, Oregon.

[4] Marshal Jones, Biologist, Office of Endangered Species (FWS), Reg. 4, Atlanta, Georgia.

[5] Jim Bartel, Botanist, Office of Endangered Species (FWS), Reg. 1, Sacramento, California.

[6] Dick Dyer, Botanist, Office of Endangered Species (FWS), Reg. 5, Newton Corner, Massachusetts.

[7] Marshal Johnston, Botanist, Department of Botany, University of Texas, Austin.

with leafy spurge, and 9 of the 12 species could act as bridges to rare review species. *E. purpurea* and *E. telephiodes* are test plants because they are under review and are closely related to leafy spurge (subgenus Esula spp.). *E. maculata*, *E. supina*, and *E. heterophylla* L. are test plants because they are at times reported as weedy (Dunn 1979). *E. marginata* (snow on the mountain) and *E. corollata* L. (flowering spurge) and *E. heterophylla* (fire plant) are cultivated as ornamentals (Bailey 1951). An effort has been made to select native species that possess a number of the desired characteristics to reduce the number of test species needed.

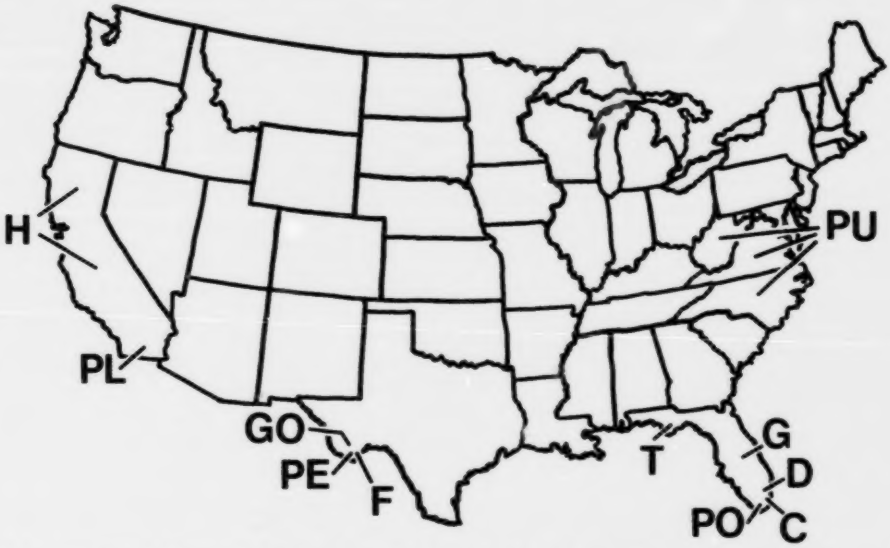

Fig. 4. Distribution of rare spurges which are under review for legal protection as threatened or endangered status. H = *Euphorbia hooveri* L.C. Wheeler, PL = *E. playsperma* Engelm., PE = *E. perennans* (Shinners) Warnock & M. Johnst., GO = *E. golondrina* L.W. Wheeler, F = *E. fenderli* Torr. & Gray var. *triligulata*, T = *E. telephiodes* Chapm., PU = *E. purpurea* (Raf.) Fernald, G = *E. garberi* Engelm. ex Chapm., D = *E. deltoidea* Engelm. ex Chapm., C = *Chamaesyce cumulicola* Raf., PO = *C. porterana* Small.

The Insects

Hyles euphorbiae is a large hawk moth whose larvae are defoliators. The moth, which was first released in North America in 1961, occurs on numerous *Euphorbia* spp. throughout its native Eurasia (W. Europe to northern India) (Harris 1984). During the pre-introduction host specificity testing conducted on the moth, two North American native spurges, *E. maculata* and *E. marginata*, were tested and accepted as hosts (Harris, unpubl. rept.). Harris felt that most species of *Euphorbia* were potential hosts. *E. maculata* belongs to the subgenus Chamaesyce and *E. marginata* is a member of the subgenus Agaloma. This acceptance of members of these subgenera, coupled with ready acceptance of European subgenus Esula species, suggests that despite only two North American spurges being tested, the moth could attack most spurge species on this continent. Table 5 summarizes the known host specificity range for this moth and the other insects which will be discussed. *H. euphorbiae* has recently been found to be established on leafy spurge in Montana (N. Rees, USDA, Bozeman, Mont., pers. comm.) from stocks which probably originally were collected from *E. cyparrissias* L. or *E. seguierana* Necker in Europe (Harris 1984). Additional establishments of the moth have been obtained on leafy spurge in Montana in 1984 (N. Rees, pers. comm.), from material released in 1983, which had been collected by USDA Rome laboratory researchers from *E. waldsteinii* in Hungary.

Chamaesphecia tenthrediniformis (Schifferraüller) (Lepidoptera: Ageriidae), is a clearwing moth which bores the roots of leafy spurge. In its native Europe, *C. tenthrediniformis* is known from *E. esula sensu stricto* and possibly *E. velenovski* (Harris 1984). In the moth's host specificity testing, *E. marginata* was the only North American spurge tested. It did not support development (Schroeder 1969). Releases of this moth began in 1970 and continued for several years. When establishment failed to occur despite repeated attempts, additional laboratory studies were done. This work showed that the larvae were unable to use the spurge forms that are the main problem (Harris 1984). As mentioned above, the principal leafy spurge is thought to be a hybrid of *E. esula sensu stricto* and *E. waldsteinii* (Dunn and Radcliffe-Smith 1980). Since *C. tenthrideniformis* does not use *E. waldsteinii* even when it grows with acceptable *E. esula* (Harris 1984), *E. waldsteinii* may be contributing some quality to the hybrid which is repellent. It is also possible that some *E. esula* quality, required by the moth, is absent. For whatever reason, *C. tenthrideniformis* appears to be too narrow in its host specificity to attack the hybrids and forms of North American leafy spurge.

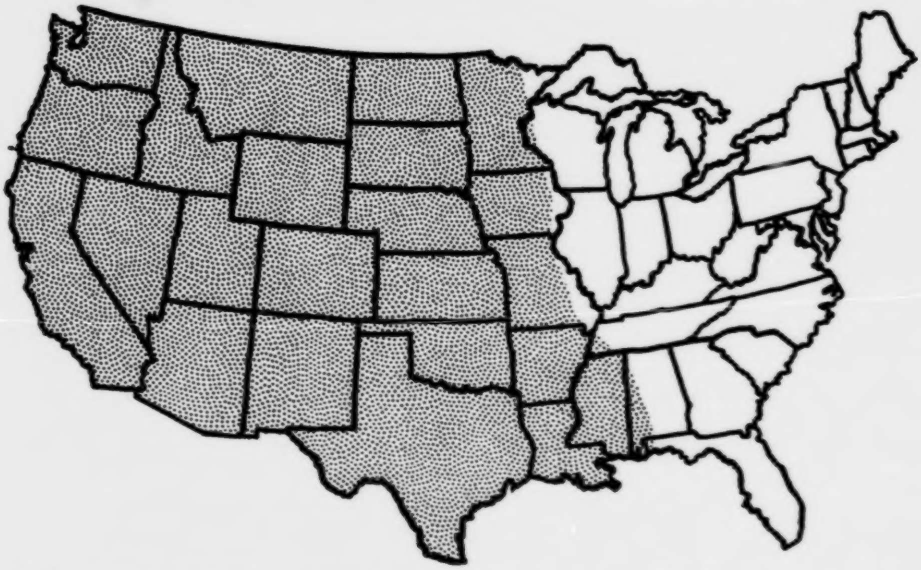

Fig. 5. Distribution of *Euphorbia spatulata* Lam., a subgenus esula species which could serve as a bridge from leafy spurge to the rare spurges under review.

Oberea erythrocephala (Schr.) (Coleoptera: Cerambycidae), is a stem- and root-boring beetle of leafy spurge. It is recorded from a number of perennial *Euphorbia* spp. from south and central Europe through Asia Minor and south Siberia (Harris 1984). Four native North American spurges (*E. corollata* and *E. marginata*, subgenus Agaloma; *E. maculata* and *E. supina* Ait.*, subgenus Chamaesyce) were test plants in egg transfer experiments. None of these plants supported development (Johnson 1979), which suggests a host plant specificity level below the genus level. Not enough testing was done, however, to predict the degree of use of North American spurges. Since larvae of *O. erythrocephala* overwinter in roots and continue to feed in roots the following spring (Schroeder 1969), this beetle probably would require perennial hosts. Fifty of the 107 spurges native to North America are perennials. Releases of this species began in 1979 and have continued through the past season. Introductions of *O. erythrocephala* collected from *E. cyparissias*, *E. seguierana* and *E. esula* in Europe, have done poorly. The larvae appear to be staying in the roots at least two years instead of the normal one and are producing few adults (only one has been recovered to date) (Harris 1984; N. Rees, pers. comm.). *O. erythrocephala* collected from *E. waldsteinii* in Hungary and released as adults in Montana in 1983, have produced adults in 1984 (N. Rees, pers. comm.).

**E. supina* is currently listed (Table 1) as a synonym of *E. maculata* because it was included in the original description of *E. maculata* (USDA, SCS 1982). These plants have frequently been treated as separate species and are probably biologically distinct.

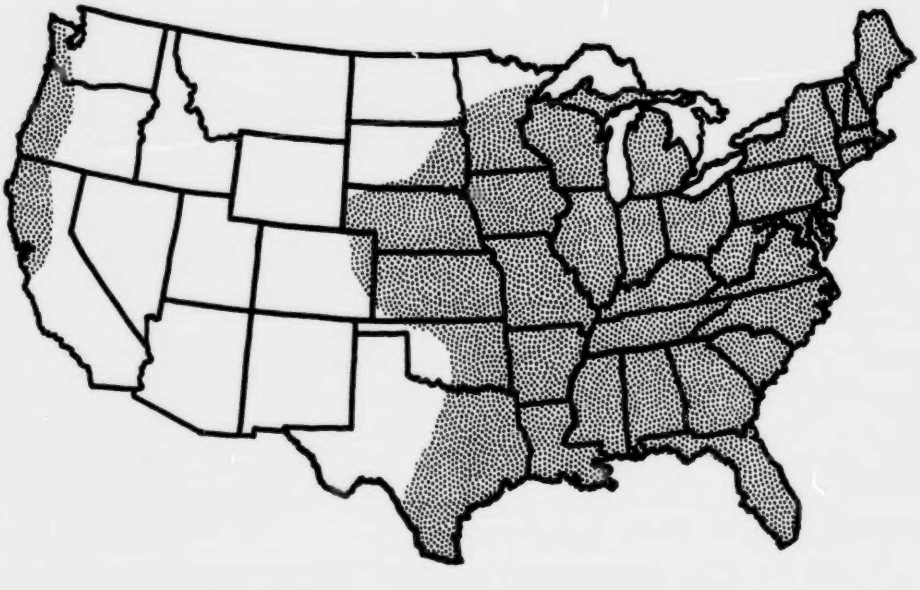

Fig. 6. Distribution of *Euphorbia maculata* L., a subgenus chamaesyce species which could serve as a bridge from leafy spurge to rare spurges under review.

Lobesia euphorbiana (Freyer) (Lepidoptera: Tortricidae), is a tip-webbing moth which is recorded from a number of *Euphorbia* spp. in Europe and Asia Minor. Literature on locality and host records for *L. euphorbiana* are confused because of the presence of *Lobesia occidentalis* Falk., a recently recognized sibling species (Harris and Soroka 1982). Eleven native spurges were tested in the host specificity testing of *L. euphorbiana*. Nine of these species including the subgenus Esula review species *E. purpurea* and *E. telephiodes* appear to support development. (The details of the host specificity testing for *L. euphorbiana* as well as *Bayeria capitigena* [Bremi] [Diptera: Cecidomyiidae] and *Aphthona flava* Guill. [Coleoptera: Chrysomelidae], discussed below, against native spurges will be published elsewhere.) The spurges accepted by this moth represent three of the four *Euphorbia* subgenera present in North America, which contain virtually all the native spurges including the rare species under review. *L. euphorbiana* is a multivoltine insect which develops readily on both annual species and perennial spurges.

This moth is cleared for release in Canada. A release of a few moths was made in Saskatchewan in 1983, but no establishment occurred (Maw 1984).

A. flava is a flea beetle, adults of which feed on foliage of leafy spurge and whose larvae feed on and within roots of the plant (Sommer and Maw 1982). This beetle is one of 27 *Aphthona* spp. that have been recorded to be associated with the genus *Euphorbia* in Europe (Sommer and Maw 1982). Three of these species, *A. cyparissiae* (Koch), *A. czwalinae* Weise, and *A. abdominalis* (Duftsch.), are being evaluated for potential use against leafy spurge. *A. flava* is recorded from five perennial *Euphorbia* spp. in its native range, which is from Italy north and east through Austria, Yugoslavia to Bulgaria, Rumania, and Russia (Sommer and Maw 1982). *A. flava* has been tested against 10 native North American *Euphorbia* spp. to try to predict its potential host range. In adult feeding, oviposition and development tests, which are almost complete, it appears that four subgenus Esula spp. are acceptable laboratory hosts. The two subgenus Esula spp. under review (*E. purpurea* and *E. telephiodes*) were not accepted as hosts. Although development was obtained on the annual species *E. spatulata* (by replacing plants they had killed) *A. flava* would probably need perennial species in nature. From this laboratory testing, it appears that *A. flava* has a host plant specificity level somewhat below the subgenus Esula. Since there are 11 perennial subgenus species, including *E. purpurea* and *E. telephiodes* which appear unacceptable, *A. flava* may be able to use no more than nine native spurges.

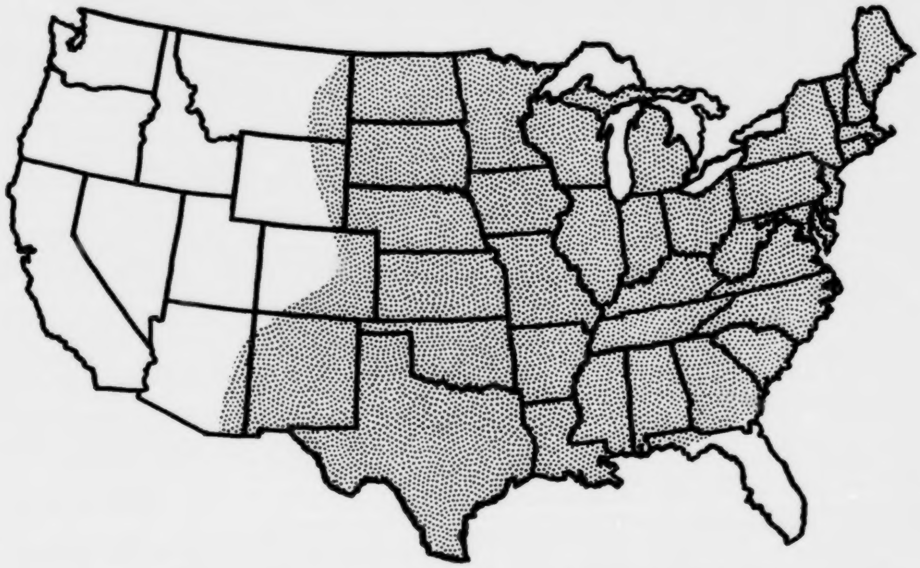

Fig. 7. Distribution of *Euphorbia marginata* Pursh, a subgenus agaloma species, which could serve as a bridge from leafy spurge to rare spurges under review.

B. capitigena is a midge which galls the meristematic shoot tips of leafy spurge. It is widely distributed in Europe and has been recorded to use at least eight *Euphorbia* spp. in nature (Pecora 1984). In host specificity tests, 11 North American *Euphorbia* spp. were presented to the midges for oviposition and development. The midges laid eggs and completed development to the adult stages on four subgenus Esula spp. As with *A. flava*, the review species, *E. purpurea* and *E. telephiodes*, were not accepted as

Table 4. Native europhorbias used in host specificity testing.

Species	Habit	Subgenus	Sympatric with leafy spurge	Potential bridge	Endangered species	Weed	Ornamental
Euphorbia heterophylla L.	Ann.	poinsettia	X	X		X	X
E. cyathophora Engelm.	Ann.	poinsettia	X	X			
E. maculata L.	Ann.	chamaesyce	X	X		X	
E. serphyllifolia Pers.	Ann.	chamaesyce	X	X			
E. supina Raf.	Ann.	chamaesyce	X	X		X	
E. robusta (Engelm.) Small	Peren.	esula sec. esula	X	X			
E. spatulata Lam.	Ann.	esula sec. galarrhoei	X	X			
E. purpurea (Raf.) Fernald	Peren.	esula sec. not placed	X		X		
E. telephiodes Chapm.	Peren.	esula sec. ipeccacuahae			X		
E. incisa Engelm.	Peren.	esula sec. esula	possibly				
E. marginata Pursh	Ann.	agoloma	X	X			X
E. corollata L.	Peren.	agoloma	X	X			X

Table 5. Known host plant specificity levels for the leafy spurge insects.

Insect species	No. of native spurges		subgenus	subgenus	subgenus	subgenus	No. of potential hosts	
	tested	*accepted*	esula	agaloma	poinsettia	chamaesyce	native	rare
Hyles euphorbiae (L.) **(Sphingidae)**	2	2	X	X	?	X	<110	<11
Chamesphecia tenthrideniformis (Schif.) **(Aegeriidae)**	1	0	X[1]	?	?	?	may be monophagous	
Oberea erythrocephala **(Schrank)(Cerambycidae)**	4 partial	0	X	?	?	?	<49	<6
Lobesia euphorbiana **(Freyer)(Tortricidae)**	11	9[2]	X	X	—	X	<110	<11
Aphthona flava Guill. **(Chrysomelidae)**	10	4[2]	X	—	—	—	<9	0
Bayeria capitigena (Bremi) **(Cecidomyiidae)**	11	4	X	—	—	—	<19	1

[1] Subgenus esula acceptance on the basis of leafy spurge (*sensu lato*) feeding.

[2] Species appear to support full development but all testing not completed.

hosts by this midge. *B. capitigena*'s level of host plant specificity is probably below the subgenus Esula level. Both annual and perennial species within that group support development and could become hosts for this multivoltine gall midge. Table 5 summarizes the known host specificity levels for the insects which have been discussed.

Discussion

To what degree biological control agents introduced for leafy spurge would use native spurges depends not only on a taxonomic host specificity level and laboratory acceptance, but many other factors including their dispersal ability, habitat preferences, climatic tolerances, and other unknown specifics of both the candidate insects and the potential hosts. Primary among these is the agent's climatic tolerance. This is particularly relevant to their use of non-target native spurges since most of these species are southern in distribution, whereas leafy spurge occurs in the colder parts of North America. Leafy spurge occurs almost entirely above the 0°C mean January isotherm, whereas most of the principal leafy spurge biological control agents (*L. euphorbiana*, *O. erythrocephala*, *H. euphorbiae*, *A. flava*, and *B. capitigena*) range south to the climatically mild areas of northern Italy, which is below the 0°C mean January isotherm (Thrower 1968). By matching the temperature data for some of the more southern localities in which the leafy spurge insects live in Europe with comparable places in North America (Walter and Lieth 1967), it could be inferred that these insects probably could live in areas south of the present range of leafy spurge in the U.S., including Texas, and possibly even northern Florida. While this information aids our ability to predict which of the native spurges might become hosts, these predictions are, considering the level of knowledge about both the insects and plants involved, rather simple estimates of risks.

Just what the actual levels of risks are and what damage to or even the elimination of some native spurges would mean are complex issues. These issues relate not only to the scientific possibilities and effects but also to the interest and values of different segments of our society. These issues are explored more fully in Turner (1985).

Whether a native non-target plant can be seriously reduced or eliminated by an introduced biological control agent is a matter of debate. Generally prey-specific 'predator' species are not thought to be able to drive their hosts to extinction, if their universe (environment they occupy) is large enough (Huffaker 1958). Extinction is prevented by the so-called density-dependent feedback, which causes the predator population to decline as it reduces its host to rarity. This allows the now rare host to recover. This mechanism breaks down when more than one host is involved since the predator's population level is no longer regulated by a single prey species. Very large populations of a biological control insect, generated by abundant leafy spurge could swamp a less abundant nearby native spurge, which would have little ability to regulate the agent's population level. In theory, rare species with restricted habitats would be the most likely to be damaged, since they have the lowest numbers and thus the weakest regulating feedback mechanism.

It has been suggested that the rare spurges will be protected from leafy spurge biological control agents by being difficult to find. The mobility and host-finding abilities of biological control insects, which varies greatly, will determine whether the rare species could be found. *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae), an introduced biological control insect of *Silybum* and *Carduus* thistles, has successfully colonized rare native *Cirsium* spp. which are quite distant from its weed hosts (Turner, Pemberton, and Rosenthal, USDA Albany, Calif., unpubl. data).

Many insects prefer the rarest of their host plants (Cates 1981). If it is expected that an introduced insect can significantly damage and reduce leafy spurge, to be consistent, it must also be expected that native spurges, which are within the host range of, and exposed to particular introduced insects, could also be damaged and reduced.

The significance of the reduction or loss of native spurges relates to their ecological position, which is poorly known. Since most North American spurge species are small and herbaceous, few figure importantly in the physical structure or energetics of their communities. *E. misera* Benth., a subgenus Agaloma shrub, is considered to be a characteristic component of coastal sage succulent scrub and coastal dunes (Barbour and Major 1977) of southern California and Baja, Mexico. *E. corollata* is listed as a component of the Oak Savanna Community (*Quercus–Andropogon*) of Wisconsin, Minnesota, and North Dakota (Kuchler 1964). The unusual and unique chemistries of spurges suggest their probable involvement in complex ecological interactions. In Europe, where more is known about the ecology of *Euphorbia* spp., there are large numbers of specialist insects, which use *Euphorbia* spp. as hosts, including the unique hemipteran family Stenocephalidae (Miller 1971).

Perhaps more important than the ecological value *per se* are the plants themselves and not their roles. This appears to be the situation with rare and endangered species, which have comparatively fewer environmental interactions and functions. These plants have been given increased value by society at large, via Congressional legislation. The new legal and political value given these plants could have important implications for the biological control approach, if endangered species were to be attacked by biological control agents. Beyond, and yet a part of, the legal concern for species, is a moral concern which relates to the integrity of species. Exponents of this viewpoint say that other life forms have the 'right' to exist and that we should consider and safeguard their welfare, as we go about our activities.

By and large, the concern for species is probably more of a concern for present or potential practical resources for human use, than for the integrity of species. The only native *Euphorbia* spp. which currently have economic value are three ornamentals: *E. corollata* (flowering spurge), *E. marginata* (snow on the mountain) and *E. heterophylla* (fire plant). In northern Mexico, west of the Big Bend area of Texas, is the candelilla wax plant (*E. antisyphilitica* Zucc.), which provides waxes for local consumption and export to the United States (Janick *et al.* 1969). A number of other species in different parts of the world are used for the gums and resins they produce (Schery 1972). Since the advent of the oil crisis, there has been discussion and research on the use of *Euphorbia* spp. as potential energy plants (Calvin 1978). The plants involved thus far (*E. tirucalli* L. and *E. lathyrus* L.) are not native and do not at this point appear to be economically feasible crops (Sachs *et al.* 1981). Some of the native spurges could be economically valuable in the future, considering the energy-rich hydrocarbons, waxes, resins, drying oils, and other useful compounds which are known to occur in some *Euphorbia* spp. The decision to introduce biological control insects to the U.S. rests with a committee of Federal scientists who evaluate the research data on candidate insects, native plant considerations, and the potential effects of the proposed introductions.

Conclusions

Few biological control of weeds projects have the degree of potential use of native plants by introduced insects which occurs in the leafy spurge project. Through selection of target plants for research which have few or no native relatives, this problem can be reduced or avoided. This is not to say that particularly difficult weeds such as leafy spurge, for which there are limited control options, should not become targets for biological control; they can be. It should be expected, however, that plants with large numbers of native relatives will require more research to evaluate host range and other undesirable effects, and that fewer natural enemy options will exist, because of the need for higher levels of host specificity.

There are large differences in the host plant specificity levels of the leafy spurge-feeding insects. The research strategy is to select, among these, species which meet two criteria: (1) they are broad enough in host range to accept the diverse forms and hybrids of leafy spurge; and yet (2) narrow enough to exclude use of most native spurges, and the rare species under review in particular.

Neither *C. tenthrediniformis* (which is too narrow in its host range) or *L. euphorbiana* (which is perhaps too broad) seem to be suitable agents for leafy spurge control. It appears however, that both *B. capitigena* and *A. flava*, with host plant specificity levels below the subgenus level, meet these criteria. These insects, and probably other as yet unknown organisms, may begin to reduce leafy spurge abundance and yet allow researchers to remain attentive to the native spurge concerns.

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Conflict of Interest in Biological Control of Weeds in New Zealand

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Abstract

The role that conflicts of interest have played in the development of projects for biological control of weeds in New Zealand in the past is discussed. Particular reference is made to projects for control of blackberry (*Rubus fruticosus*), sweet briar (*Rosa rubiginosa*), manuka (*Leptospermum scoparium*) and gorse (*Ulex europaeus*). Our present policy and approach to resolving conflict situations is also discussed in the context of how weed species are selected as targets for biological control attempts.

Conflits d'Intérêts dans la Lutte Biologique Contre les Plantes Nuisibles en Nouvelle-Zélande

L'auteur examine le rôle qu'ont joué les conflits d'intérêts dans l'élaboration des projets de lutte biologique contre les plantes nuisibles en Nouvelle-Zélande dans le passé, en se référant plus particulièrement aux projets de lutte contre les ronces (*Rubus fruticosus*), l'églantier odorant (*Rosa rubiginosa*), le manuka (*Leptospermum scoparium*) et les ajoncs (*Ulex europaeus*). L'étude porte également sur les politiques et les méthodes actuelles de résolution des conflits relatifs à la méthode de sélection des espèces de plantes nuisibles cibles pour des tentatives de lutte biologique.

Introduction

Conflicts of interest were recognized from the outset when several projects aimed at tackling New Zealand's weed problems through biological control were initiated in the 1920s. Workers appreciated the necessity for reliable host-specificity data, and refrained from introducing insects when there was any danger of damage to non-target plants. In the case of gorse, *Ulex europaeus* L. (Leguminosae), recognition of its beneficial qualities caused prospective biological control agents to be restricted to flower- and seed-feeders. Most of the weeds which now cause serious problems in New Zealand were purposely introduced during the last century for their beneficial qualities, or to remind homesick settlers of Europe. Typically, under favourable climatic conditions, released from competitive pressure of other species and unrestrained by their native fauna, these weeds proved more aggressive than in their native range, growing faster and attaining greater size. Costs of weed control to agriculture and forestry in New Zealand are extremely high: Hill (1983*b*) calculated that for gorse alone, the current annual costs of control are in excess of $14 million.

In the past, biological control efforts have been directed against weeds whose control costs are greatest, but now that New Zealanders have developed a greater appreciation of their country's unique native flora, there are aesthetic as well as economic reasons for attacking introduced plants. Having suffered the consequences of well intentioned but unfortunate introductions of exotic species which have become pests, the public is understandably cautious of proposals to introduce further exotic organisms, beneficial or otherwise. Thus good publicity is essential to communicate the long-term advantages of biological control. To an environmentally conscious public, the concept of biological control is attractive. Apart from reducing the necessity for, and hence the cost of control by conventional means, the prospect of reduced dependence on ecologically damaging chemicals seems highly desirable.

However, we have to take care that our 'clients' are aware of the limitations of the biological method of control: that we aim only to reduce weed populations, not to eliminate them, that we cannot accurately predict the level of control that can be achieved, and that the time taken from the initiation of a project to its fulfillment may be lengthy. To justify the importation and release of a new insect species it is essential that results of specificity testing should be conclusive and convincing, to reassure those who are concerned about the potential danger to non-target plants. The public should be aware also of the safety record of our past work: none of the species introduced for weed control have been reported as damaging desirable plants. While cinnabar moth (*Tyria jacobaeae* L.) (Lepidoptera: Arctiidae) may (as indicated by host-specificity tests carried out prior to its release) occasionally be found on garden *Cineraria* spp. (Compositae), damage to the plant is insignificant.

Case Histories

We shall now consider several of the weed species for which biological control programmes have been undertaken, and the role that conflicts of interest have played in the development of these projects.

Blackberry: Rubus fruticosus *L. (Rosaceae)*

During the search for candidate insects for blackberry control, a review of the species recorded from this weed in other parts of the world was undertaken (Miller 1970). Insects attacking *Rubus* species in Hawaii, North America, Great Britain and Europe, and South Africa comprised 12 species of Hymenoptera, 6 species of Coleoptera, 12 species of Lepidoptera, 8 species of Diptera and 1 hemipteran. Unfortunately blackberry is closely related to a number of important crop plants, and most insect species recorded from *Rubus* were also recorded from cultivated plants. Between 1927 and 1931, however, consignments of five insect species attacking blackberry were imported into New Zealand (Miller 1970). Of these, two (from North America) were unable to be reared satisfactorily, and work with the remaining three (all from Europe) was discontinued when it was found they fed on economic plants.

Larvae of *Thyatira batis* (L.) (Lepidoptera: Thyatiridae) defoliated raspberry, loganberry and strawberry in tests under quarantine, while larvae of *Dasineura plicatrix* (H. Loew) (Diptera: Cecidomyiidae) attacked raspberry foliage. *Coraebus rubi* (L.) (Coleoptera: Buprestidae) was considered very promising since its stem-boring larvae were highly damaging to blackberry, but had only one other recorded host, the China rose, *Rosa indica* (Rosaceae). Nurserymen were consulted to ascertain that this species was not grown as a stock to any extent in New Zealand, but while tests showed that larval infestation did not occur on raspberry, loganberry or on four species of *Rosa*, adult beetles fed freely on a number of rosaceous crop plants. Thus release of this insect was ruled out, and work on biological control of blackberry was discontinued.

The redberry mite, *Acalitus essigi* (Hassan) (Acari: Eriophyidae), which causes redberry 'disease' in blackberries and raspberries first appeared in New Zealand in 1946

(Hamilton 1949). It was not introduced intentionally for control of blackberry, however, and Miller (1970) suggested that it may have arrived on apple stocks imported from England.

While in the interests of the country's berryfruit growers no further work on biological control of blackberry is planned in New Zealand, the Australians have been working with the European blackberry rust fungus, *Phragmidium volaceum* (C.F. Schultz.) Winter (Uredinales) (Hasan 1981). Since a rust fungus, once established in south-eastern Australia would be expected to reach New Zealand within a few years, New Zealand's interest in the project has been recognized. There has been regular contact between Australia and New Zealand throughout the project and it is unfortunate that, as the result of an apparently illegal introduction, the rust is now established widely in Victoria (Marks *et al.* 1984).

Sweet Briar: Rosa rubiginosa *L. (Rosaceae)*

Sweet briar was deliberately introduced into New Zealand by the early settlers, probably for decorative purposes, but its weedy properties had become apparent by 1900 when it was declared a noxious weed throughout the country (Molloy 1964). During the 1950s, following a spectacular decline in rabbit numbers, sweet briar became an increasingly aggressive scrub weed, particularly on dry tussock grassland country (Molloy 1966). Until the decline in rabbit numbers, grazing by rabbits and sheep checked growth of seedlings and young plants. No effective means of chemical control was immediately apparent (Dingwall 1962), and from 1962 the Commonwealth Institute of Biological Control investigated over 400 species of insect attacking sweet briar and its close relatives in Europe (Given 1967*a*). Few showed indications of being sufficiently specific, however. Not only is sweet briar closely related to horticultural crop plants such as apples, plums, apricots and raspberries, but cultivated varieties of *Rosa* are widely grown for gardens.

The most promising candidate for introduction was thought to be the gall wasp *Dipolepis rosae* (L.) (Hymenoptera: Cynipidae). It was anticipated that the National Rose Society would be concerned about its use, however, as the insect is not restricted to *R. rubiginosa*, but is recorded from a number of species of wild roses, as well as occurring occasionally on cultivated roses. It was observed that galls were much more numerous on roses growing under stress conditions where growth was slow, usually in areas with a warm, dry climate. Schroeder (1967) showed that *D. rosae* produced the greatest number of galls in localities with average summer temperatures above 18°C and less than 760 mm rainfall p.a. He suggested that cultivated roses, growing under good conditions, were able to suppress gall formation in almost all cases.

In 1968 it was decided to discontinue the sweet briar project since no highly effective and specific insect control agents had been found. A factor contributing to this decision was that no suitable quarantine facilities were at that time available in New Zealand to house the lengthy specificity testing programme that would have been essential prior to release of any insect.

The rose hip chalcid *Megastigmus aculeatus* (Swederus) is widespread on sweet briar throughout New Zealand (Molloy 1964). No assessment has been made of its effect on seed production here, although indications from its native Europe (Eichhorn 1963) are that infestation rates are low. It is unfortunate that none of the five species of insect studied in rose hips in Europe showed signs of being very effective (Eichhorn 1963), since growers of cultivated roses are unlikely to be so concerned about seed feeders.

Manuka: Leptospermum scoparium *Forst. (Myrtaceae)*

During the 1940s large areas of the native scrubweed, manuka, were dying as a result of attack by the scale insect *Eriococcus orariensis* Hoy (Homoptera: Eriococcidae). This species, and the closely related *E. leptospermi* Maskell are thought to have been self-introduced from Australia, windborne across the Tasman sea (Hoy 1959). Farmers, keen to utilize an organism which might destroy what was to them a troublesome woody weed, actively transferred infected material from original infestation sites in Canterbury to other parts of the country so that by 1954 the scale insect was widely distributed on manuka through both North and South islands of New Zealand (Hoy 1954). Hoy (1949) observed that although the scale insect was capable of killing stands of manuka, this was a gradual process taking 6–7 yrs from the time of initial infestation. Given (1967*a*, *b*) noted that although the scale was spectacularly effective in controlling manuka for some years, it apparently became less effective. This loss of influence was attributed to the insect pathogenic fungus *Myrangium thwaitesi* (Dothideales).

Hoy (1953) remarked that there was considerable controversy regarding the wisdom of using a biological control agent against a substantial member of the indigenous flora. Manuka plays a significant role in natural regeneration of native forest and is also important in preventing erosion on steep hill country, as well as providing good firewood and a measure of shelter for stock (Hoy 1949). During a survey in south-eastern Australia and Tasmania, Hoy (1959) discovered that there was at least one other species of *Eriococcus* which, should it be introduced into New Zealand, could result in even greater damage to manuka. But because of reservations concerning the merits of manuka as against its weedy properties, no introductions were considered.

Gorse: Ulex europaeus *L. (Leguminosae)*

Gorse was purposely introduced into New Zealand last century as an inexpensive and fast-growing hedging plant, but spread rapidly throughout the country to be declared a noxious weed in 1900 (MacCarter and Gaynor 1980). When insects were considered for gorse control in the 1920s, gorse was still recognized as a valuable shrub for fencing, shelter and even fodder (Miller 1970), so the search in Europe was confined to those species which attacked flowers and seeds. Thus it was hoped to contain the spread of the weed without interfering with its growth in situations where it was considered beneficial. Of the usable species discovered which were restricted to gorse, the most information was available on the gorse seed weevil, *Apion ulicis* Forst. (Coleoptera: Apionidae). The gorse seed weevil was introduced in 1926 and it established well to become one of the most common insects in New Zealand (MacCarter and Gaynor 1980). Its effect on seed production is not known, but while Miller (1970) suggests that there may be two generations/yr under New Zealand conditions, Cowley (1983) has found that around Auckland, at least, there is only one generation/yr, and that the winter crop of seeds (from February to May) is unattacked by the weevil. *A. ulicis* is parasitized by a *Pteromalus* sp. (Hymenoptera: Pteromalidae) of unknown origin (P. Syrett, unpubl. data).

The current situation is that while it has been shown that gorse can be useful as a pioneer species in the regeneration of native vegetation (Hackwell 1980), and is still used to a very limited extent for hedging and shelter, it is considered to be one of the worst and most costly weeds of agriculture and forestry (Hill 1983*b*). Thus Entomology Division, DSIR, has renewed its efforts towards biological control of gorse. Several species are under consideration for introduction (Hill 1983*a*).

In response to active publicity for this work by the DSIR, New Zealand beekeepers have expressed concern that biological control of gorse will result in the loss of a valuable pollen source. To counter this fear, we were represented at the 1983 New Zealand Beekeepers Conference (Hill 1983*b*). Hill made it clear that, with the maximum level of control likely to be achieved, gorse would still remain a common plant, and that it was even less likely to experience temporary removal from local areas than by current conventional control measures.

Concern has also been expressed about the possible use of the gorse mite, *Tetranychus lintearius* Dufour. (Acari: Tetranychidae), for control of gorse. While this mite is the only species known to kill gorse bushes (Hill 1983*a*) it is a close relative of the two-spotted mite, *T. urticae* Koch, a serious pest of horitcultural crops (Scott 1984). Thus in addition to exhaustive host-specificity testing, it is necessary to ensure that the gorse mite will not hybridize with *T. urticae*, since the introgression of gorse mite genetic material into New Zealand populations of the pest mite (with the possibility of improved performance of the pest mite) would be regarded as potentially damaging. These studies are currently in progress at CIBC, U.K. (R.L. Hill, unpubl. data).

Discussion

Nearly 60 yrs after the inauguration of biological control of New Zealand weeds by means of insects we have still to resolve the problem of how best to allocate our resources and which weeds we should work on in the future. While we are committed to our present projects, we should clarify the principles on which future projects will be selected. Currently the weeds we have selected to work on are those whose control costs by conventional means are high, and which cause serious problems throughout the country. We are aware of the limitations of these criteria, but true economic costs of a weed and the economic gains through biological control are extremely difficult to obtain. To justify allocation of further resources for biological control work it is necessary that success be demonstrated. New Zealand's early projects on biological control of weeds illustrate the limitations imposed by conflict of interest: both the blackberry and sweet briar programmes were concluded without the release of a single insect, following the investment of many years' work. Scientifically such work may not be wasted, however. With the passage of time, changing interests may even lead to the removal of the conflict and projects being reactivated. Practically, however, the public looks for results, and since conflict of interest imposes such limitations on our work, it is an important factor to be considered when new projects are contemplated.

Conflicts may be divided into three classes: (*a*) those where the weed status of the target plant is in question; (*b*) those where the conflict arises through the risk to non-target plants; and (*c*) those relating to programmes against native weeds where ecological and conservation aspects are important. There has been some slight conflict over our thistle control programme. Insects have been released against nodding thistle (*Carduus nutans* L.; Compositae) and Californian thistle (*Cirsium arvense* [L.] Scop.; Compositae) (Jessep 1975, 1981; Jessep unpubl. data). Neither thistle species is closely related to any economic plant grown in New Zealand, and there are no native species of either genus in New Zealand. However beekeepers have expressed concern about nodding thistle which they regard as a valuable source of nectar; since *C. nutans* is classified as a noxious plant, and is presently controlled by chemical means, Hill (1983*b*) has pointed out that nectar production (from thistles and clovers) is more likely to be reduced by the current applications of herbicide to pastures than by developing biological controls.

Other weed species which have recently been brought to our attention as candidates for future biological control programmes are old man's beard (*Clematis vitalba* L.; Ranunculaceae) and hawkweeds. *C. vitalba* is a serious problem in native bush reserves where it smothers and kills trees (Atkinson 1984). It is difficult to control with herbicide without damaging native vegetation, so that current control measures are highly labour intensive. Biological control is thus an attractive option, but any prospective control agent must be specific to *C. vitalba* and not attack the 11 native *Clematis* species. In addition, ornamental species are cultivated in many gardens. Thus conflicts could arise concerning the risk to non-target plants. Hawkweeds (*Pilosella* spp. and *Hieracium* spp.; Compositae) are weeds of hill and high country pasture with allelopathic properties (Makepeace 1976) and no beneficial qualities of consequence. Their taxonomy is complex, but they have no close relatives among cultivated plants nor among plants native to New Zealand. A number of rust fungi are recorded from *Pilosella* spp. and literature records show 16 species of insect occurring on hawkweeds (Scott, pers. comm.).

It is not always possible to anticipate conflicts which may arise, at the outset of a project. A plant recently added to the list of eocnomic species in New Zealand is tree lucerne, *Chaemaecytisus palmensis* (comb. ined.) (Leguminosae). Tree lucerne is being developed for hedging, is useful for shelter, forage and as a source of nectar for bees (Davies and MacFarlane 1979). This has implications for our biological control programmes against gorse and broom (*Cytisus scoparius* [L.] Link; Leguminosae) since preliminary work shows that insects otherwise specific to gorse and broom (Waloff 1968) may find tree lucerne a suitable alternative host (R.L. Hill, unpubl. data).

Native weeds have been included as candidates for biological control projects in the past. For example the sawfly *Ucona acaenae* Smith (Hymenoptera: Tenthridinidae) (previously *Antholcus varinervis* Spinola) was introduced from Chile for control of piripiri (*Acaena* spp.; Rosaceae) (Miller 1970). Its larvae cause severe damage to leaves and developing flowers. Releases were made from 1936 onwards. Initially it established well, having a marked effect on the weed, but after a few years it apparently died out. However our present policy is to concentrate our efforts towards control of exotic weed species. Before attempting to manipulate a member of the indigenous flora it is important that its ecological role be thoroughly understood; this information is not readily available for many native weeds.

Biological control is generally a long-term approach to weed control, and since our resources are very limited, it would seem most profitable to work in areas where there is a high chance of success. There are a number of factors to be considered here, but one should be to avoid any project in which a strong conflict of interest is apparent at an early stage. The Ministry of Agriculture and Fisheries (MAF) controls the introduction of new species into New Zealand. At the time an application is made to MAF as the regulating body, the destiny of each organism must be specified. This provides an early opportunity for potential conflicts to be recognized. When conflicts do arise, it is desirable that interested parties be brought together so that some balance may be achieved between the conflicting factors. While responsibility rests with us to ensure that people are aware of our work and its implications, at least some of the onus for justification of biological control projects should rest on the parties which benefit from the introductions.

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Conflicts of Interest in the Use of Grass Carp

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Abstract

In biological control of aquatic weeds with herbivorous fish, many potential conflicts exist, since the aquatic environment is generally used simultaneously for various purposes. Three examples are given of situations where conflicts are (or have tried to be) solved or prevented: in Egypt by extension, in the USA by research, and in the Netherlands by regulations. These examples can be used for conflict-counteracting scenarios in future situations; those directed towards prevention of conflicts are expected to be most successful.

Conflits d'Intérêts dans l'Utilisation de la Carpe Herbivore

La lutte biologique contre les plantes nuisibles aquatiques au moyen de poissons herbivores peut donner lieu à de nombreux conflits, puisqu'en général, le milieu aquatique est utilisé simultanément à diverses fins. L'auteur donne trois exemples de situations où ces conflits ont été résolus ou prévenus (où on a tenté de le faire): en Égypte, par des programmes de sensibilisation, aux États-Unis, par des recherches, et aux Pays-Bas, par la réglementation. On peut avoir recours à ces exemples pour concevoir des scénarios qui permettront de résondre les conflits à l'avenir; on prévoit que les méthodes destinées à prévenir les conflits donneront les meilleurs résultats.

Introduction

Herbivorous fish are biological control agents of weeds that are used on a practical scale. Many species are used or studied (van Zon 1978), but grass carp (*Ctenopharyngodon idella* Val.; Cyprinidae) is the most important because of its high ecological amplitude and its voracious and unspecific consumption (van Zon 1981; Shireman and Smith 1981; Zonneveld and van Zon 1984). For these reasons this species has often been stocked for weed control purposes, and has been subject to many different conflicts of interest. It is expected that the types of conflicts discussed below will apply equally to other phytophagous fish species when they are used for aquatic weed control.

Reasons for Conflicts

Conflicts about biological control agents in an aquatic environment develop for the same reasons as in terrestrial situations: the agent can pose a threat for areas where it is not wanted (fish cannot fly, but water itself is a perfect transportation medium!) or it can attack desirable (or not troublesome) species of plants. Chances for the latter are even larger when using fish, since this type of agent has most value when it is a non-specific feeder: aquatic weed problems are generally vegetation problems more than species problems. However, the chance that a polyphagous organism will eradicate a plant species is virtually absent, and the presence of commercially important plant species in a habitat suited for fish survival is also very limited.

There is, however, another source of conflict in the aquatic environment, and that is its multifunctional use. A water body rarely has only one function in which aquatic plants play a (positive or negative) role. In general, water bodies can be used simultaneously for agricultural purposes (irrigation, drainage, processing, etc.), fisheries, transportation, recreation, conservation (nature, landscape), and/or drinking water production. Weed control to improve one of these functions does not necessarily improve other functions, and that creates the conflicts. This is also the case in the use of mechanical or chemical methods of aquatic weed control, but even more so when fish are used. The reason for this is that more people or authorities traditionally play a role in fisheries management.

Weed control in traditional ways is often seen in the first place as a responsibility of agriculture authorities only. As soon as fish are stocked, other authorities (sometimes other ministries) also become responsible, based on existing laws or rules. Authorities often start their involvement with the release of a statement; negative statements are normally not easily corrected, and the conflict is born. This sometimes has illogical consequences: if a nature conservancy department opposes publicly use of grass carp (i.e. introduction of an exogenous animal), they in fact vote for the alternatives (chemicals), that are often clearly less suited to serve the specific interest of protection of nature.

A number of this type of conflict arise regularly. In developing countries these are generally between weed control (irrigation) and fishery authorities, whereas in Western Europe and the USA most conflicts arise between weed control authorities and nature conservancy or recreation (sport fishing, hunting) authorities. For these conflicts a few solutions have been reported that partly could be used as scenarios in future situations.

The Egyptian Approach: Extension

In Egypt, irrigation authorities want to use grass carp for weed control as an alternative to application of the toxic chemical acrolein (2-propenal), which has been reported to cause accidents and discomfort (Dubbers *et al.* 1981; Gharably *et al.* 1982; van Zon 1984). Professional fishermen utilize the canals to be stocked, and to protect the stocked grass carp the authorities considered prohibiting fishing. The fishermen, however, did not want to leave their traditional jobs. Agricultural authorities did not want them to, since freshwater fish are an important protein source for the rural population. The conflict was obvious.

An analysis of the problem, however, showed that the irrigation authorities in fact needed the fishermen for guarding and managing the stocked grass carp populations, whereas the fishermen needed to maintain those populations in such a way that weed control was guaranteed. If this did not happen, the irrigation authorities would be forced to return to use of acrolein, which was proven to be detrimental to the fisheries.

A solution for the conflict was found by granting permission to the fishermen to take out (and market) any grass carp above a certain size, as long as they put back all smaller individuals. This system raised the fishermen's income substantially and continuously (especially since endemic fish catches also improved after the discontinuance of acrolein use) and weed control was obtained.

The United States Approach: Research

In the USA a number of parties from different ministries or administrative levels are interested in grass carp: Game and Fish Authorities, Departments of Natural Resources, Universities, the Army Corps of Engineers, Weed Control Authorities, Agricultural Research Stations, commercial fish producers, etc. In different States different conflicts arose, since the opinions of the authorities were different. Sometimes Game and Fish authorities are in favour of use of grass carp and Natural Resources authorities are against its introduction; sometimes the opposite happens.

The main subject of all the conflicts, in fact, was always the same: the yes-or-no chance that grass carp could breed naturally in the States, and could become an unwanted problem (Sutton 1977; Stanley *et al.* 1978; Proceedings Grass Carp Conference 1979).

The actual 'wanted' or 'unwanted' was dependent on the working programme of the authority concerned; if, for example, Natural Resources had to deal with the control of *Hydrilla verticillata* Lf. Royle (Hydrocharitaceae) (as in Florida), they were supporters of use of grass carp, since this remedy was considered less serious than the disease. Natural Resources departments in States without *Hydrilla* in general opposed use of the fish. Game and Fish authorities were generally only strongly against use of grass carp when duck hunting was important in their area, since duck hunting will decrease with aquatic plant control. A number of lawsuits passed (with different outcomes), and the situation became unworkable.

A solution to this series of conflicts can be found through research into the actual cause of the conflicts: if natural breeding could be made impossible, most problems could be solved. Various techniques have been tested, including monosex culture, sex reversal, and sterilization, but none of them were suited for mass production. In recent years all effort has been directed toward mass production of sterile hybrids of grass carp and other cyprinids, mainly the bighead, *Aristichthys nobilis* Rich. (Miley 1980; Kilambi and Zdinak 1981; Krasznai *et al.* 1982).

The Dutch Approach: Regulations

In the Netherlands it became clear during the first experiments with grass carp that potential conflicts were to be expected between the waterboards (responsible for quantitative water management, and thus weed control), the Water Quality Authority, Nature Conservancy (responsible for the numerous small aquatic reserves in the Rhine and Meuse Delta), and/or the Anglers Association (subsidizing artificial fish breeding and stocking).

Actual occurrence of conflicts was prevented in the Netherlands by the formation of a Grass Carp Working Group, in which all parties potentially involved tried to determine under what conditions they could accept the release of the fish.

The discussions in that Working Group (and the results of research undertaken under the auspices of the Group) led to the development of the following Rules and Regulations (van Zon 1979; van der Zweerde 1983): (1) There has to be an aquatic weed problem in the water concerned (i.e. grass carp will only be stocked in problem situations); (2) There are no conservation interests in the water concerned (determined by advice from the regional advisor in question); (3) The water should be suited for fish (determined by advice from the regional fishery advisor in question); (4) The water should be fishtight, naturally or artificially (to be checked by the regional fishery advisor); and (5) The grass carp should be bought from the official Dutch fish breeding organization (which means artificially bred fish, clean from exotic parasites or diseases). This organization also takes care of the stocking of grass carp after permission mentioned above has been received.

For this procedure a special administrative procedure has been developed by the Ministry of Agriculture and Fisheries, and in practice the whole procedure runs smoothly. At the same time it is strictly forbidden for anglers to remove grass carp (as printed on their fishing permit), unless thinning-out of the stocked population in question has been agreed by the waterboard and the angler's organization.

Summary

It can be seen from the Egyptian and the Dutch cases that in principle, conflicts in the use of grass carp can be solved best by prevention. People or organizations that object to biological weed control in general expect their own interests to be injured. By getting them involved from the very start of a control programme (even in the research phase) the potential opponents not only have the possibility to bring into the programme their own specific interests, but they are also from the beginning co-responsible for results and trials. And, *qualitate qua*, they are the best persons to defend such a control programme in their own circle.

One group of conflicts is not discussed here: those between grass carp supporters (in the widest sense) and the herbicide industry. In the industrial countries this type of conflict does not normally arise, since the use of herbicides in water bodies is generally well regulated and grass carp are often stocked where approved chemicals are not effective or too expensive. In developing countries, however, these problems do exist: biological control programmes sometimes have to fight against a financially strong industrial lobby. These conflicts can best be prevented by keeping discussions open. An integrated approach is often feasible, such as the combination of grass carp with certain herbicides against marginal weeds or for plot treatment. If conflicts arise, they often cannot be solved because of lack of data. It is recommended therefore, that research on effects and/or side-effects of biological agents includes those of existing methods, instead of those of a situation without any control method. Only then an acceptable solution of the conflict is possible, based on comparison of data.

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Chapter Five
Biological Control of Thistles

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Insects and Thistle Heads: Resource Utilization and Guild Structure

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Abstract

The relationship between resource utilization (percent of flower heads attacked) and 'species packing' (number of phytophagous species within a flower head sample) is investigated for 11 European Cynareae species. The correlation between these parameters depends on the trophic strategies realized within a phytophagous guild. The two most important trophic alternatives are: (1) formation of structural or physiological galls combined with an aggregated early attack; and (2) feeding on achene and receptacle tissues. Phytophagous species of type (1) can reach high levels of resource exploitation in autochthonous insect-Cynareae complexes and have been successful in biological control projects. In guilds where species of this type occupy a dominant position, an increase in species packing only weakly augments the level of resource utilization. In guilds without dominant phytophagous species the correlation between resource utilization and species packing can be high. The possible reasons for these differences and the implications for biological weed control are discussed.

Les Insectes et les Capitules de Chardons: Utilisation des Ressources et Structure des Communautés

Les complexes d'insectes phytophages et entomophages associés aux capitules des espèces de Cynareae forment des systèmes écologiques où le flux énergétique et les interactions entre des éléments simples peuvent être étudiés de façon approfondie. Par conséquent, ces complexes constituent des modèles appropriés pour l'analyse des interactions entre la diversité et la stabilité écologiques. L'auteur fournit et analyse des données sur les taux moyens d'utilisation des ressources par les insectes de Cynareae, sur la stabilité des systèmes insectes-Cynareae et sur la structure des communautés d'espèces phytophages. Le 'tassement' des espèces est, dans un grande mesure, fonction de l'évolution et des antécédents biologiques du système insect–plante, tandis que le degré d'utilisation des ressources dépend de la stabilité de l'habitat, de l'abondance et des possibilités de prévision des populations de plantes hôtes et du degré de prédation et de parasitisme. Les corrélations qui existent entre le 'tassement' des espèces et les niveaux moyens de consommation des ressources varient grandement. Des systèmes simples qui se sont établis au cours des projets de lutte biologique contre les plantes nuisibles (par example, *Rhinocyllus conicus* — *Carduus nutans*, *Urophora affinis*, et *U. quadrifasciata* — *Centaurea diffusa*) mettent en évidence des flux énergétiques plus importants et des effets plus notables des phytophages sur les populations de plantes hôtes que dans les systèmes autochtones présentant de vastes communautés d'insectes et des chaînes alimentaires complexes. Dans tous les systèmes insect-chardon qui ont fait l'objet d'études, l'élément 'contrôle des donneurs' (selon PIMM) est dominant, c'est-à-dire que les modèles de répartition spatiale, les modèles saisonniers de floraison et les réactions physiologiques des populations de plantes hôtes ont une fonction de contrôle par rapport à la dynamique des populations des insectes phytophages. Dans les complexes autochtones insectes-Cynareae, la compétition interspécifique pour la nourriture et l'espace nécessaire aux larves constituent un facteur dominant. Sur le plan de l'évolution, cette competition est à l'origine d'une structure caractéristique des communautés dans la grande majorité des complexes insectes-Cynareae. Chaque communauté possède des espèces qui disposent d'une 'stratégie d'attaque multiple au début de la floraison', ce qui favorise le transport des assimilés dans les capitules infestés; en outre, il existe des insectes granivores solitaires qui se sont souvent dispersés outre mesure et, finalement, un groupe d'insectes pouvant opérer à plusieurs niveaux trophiques.

Introduction

The relationships between the average resource utilization by a guild of phytophagous insects and the size and structure of this guild are of interest for the biocontrol of weeds as well as for the community ecologist. Flower heads of thistles and knapweeds (i.e. members of the tribe Cynareae of the Astereae) are suitable objects for a study of such relationships. Together with their complexes of phytophagous and entomophagous insects they form 'miniature ecosystems' where the energy flow and the interactions between single components can be investigated in detail. Moreover, the taxonomic and ecological diversity of thistles and knapweeds yields possibilities for a comparative approach.

In this contribution the following three questions will be discussed for European insect-thistle head systems: (1) How predictable is the degree of resource utilization by phytophagous insects for a given Cynareae species? (2) Which factors influence the level of utilization? (3) Which relationships exist between the level of resource utilization and the composition of the guilds of phytophagous insects associated with a population of thistle heads?

Materials, Methods and Definitions

Most of the data presented here have been collected from 1962–72 when I was in charge of the 'weed section' of the European Station (Delemont, Switzerland) of the Commonwealth Institute of Biological Control. Sponsored by the Canadian Department of Agriculture and other institutions an extensive inventory of European Cynareae insects (Zwölfer 1965) was carried out. It included about 60 Cynareae species belonging to the subtribes Carduinae, Centaureinae, Carlininae and Echinopinae. Data were obtained by field observations, large-scale rearings of flower heads, and dissections of flower heads under a binocular microscope. Since 1981 much additional material became available by an interdepartmental research project of the University of Bayreuth, W. Germany (SFB 137 'Gesetzmä*β*igkeiten und Steuermechanismen des Stoffumsatzes in ökologischen Systemen', Projektbereich A: 'Die Steuerung des Energieflusses und Wettbewerbsstrategien in Nahrungsnetzen mit Primärund Sekundärkonsumenten').

Random samples containing from 50–200 mature flower heads collected at a given date at one locality form the units of our investigation. They are referred to as '*flower head populations*'. The degree of '*resource utilization*' is measured by the percent of flower heads of a sample containing phytophagous insects or showing signs of insect attack. This measure is less precise than the calculation of destroyed achenes or insect biomass/head. However, it is positively correlated with these parameters and it is meaningful for biological weed control. The term '*species packing*' represents the number of phytophagous insect species found in dissections or rearings from single flower head populations. Gall midges were not counted for the calculation of species packing, as in many samples the ubiquitous fungivorous *Clinodiplosis cilicrus* Kieff. (Diptera: Cecidomyiidae) was not assessed separately from phytophagous species such as *Dasyneura* sp. (Diptera: Cecidomyiidae). Species packing must not be confused with '*species richness*' which means the total number of species associated with a host plant and which is a function of the observation area and/or the intensity of sampling (Lawton and Schröder 1978).

Resource Utilization and Species Packing

If the relationship between resource utilization and species packing is analyzed by scatter diagrams (Fig. 1) or by calculating regression and correlation coefficients (Table

1), considerable differences are found between single Cynareae species. In the great majority of the investigated plant species there exists a statistically highly significant correlation between these variables, but in *Cirsium vulgare* (Savi) Ten. and in *C. oleraceum* (L.) Scop. the correlation can statistically not be proved. The correlation coefficients vary widely: in *Centaurea solstitialis* L. the degree of species packing explains almost 85% of the variation in resource utilization; in *Centaurea scabiosa* L. 55% can be explained. In the remaining species, however, these values are much lower (Table 1). The slopes of the regression lines are highest in *Centaurea scabiosa*, *Cirsium arvense* (L.) Scop., and *Carlina vulgaris* L., moderately high in *Centaurea jacea* L., *C. solstitialis*, *Carduus nutans* L., and *Cirsium heterophyllum* Hill, and low in the remaining Cynareae species. The most striking difference is found in the intercepts: in one group (*Cirsium vulgare*, *C. oleraceum*, *C. heterophyllum*, and *Carduus nutans*) their values are high; in another group (*Centaurea maculosa* Lam. and *C. jacea*) they are moderately high; and in a third group (*Carlina vulgaris*, *Cirsium arvense*, *Centaurea diffusa* Lam., *C. solstitialis* and *C. scabiosa*) they are low. Between the intercepts and the average levels of resource utilization exists a positive correlation ($r = 0.6780$, $p < 0.05$), whereas the correlation between intercepts and the correlation coefficients of the analysed Cynareae species is negative ($r = -0.8208$, $p < 0.01$). Also with increasing intercept values the slope values

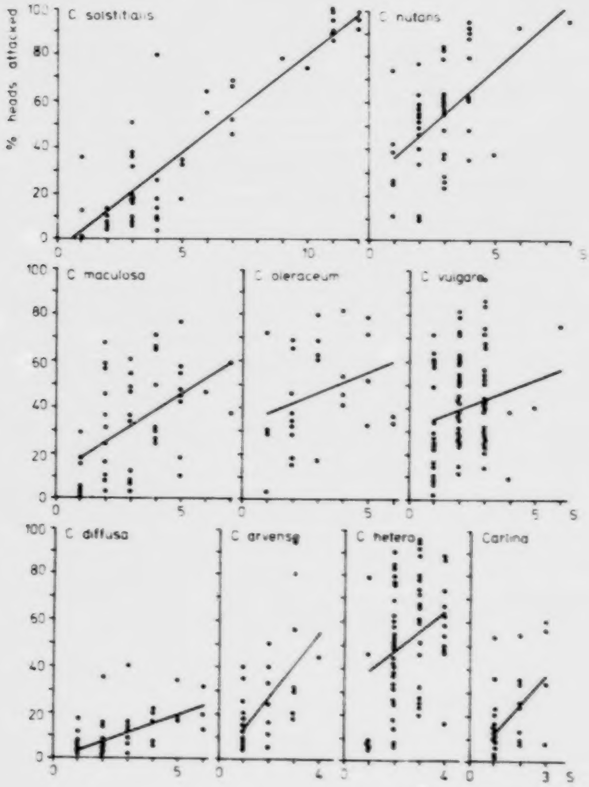

Fig. 1. Scatter diagrams of resource utilization plotted against species packing. S = species packing. Each dot represents a flower head population of 50–200 heads.

tend to decrease, but this relationship ($r = -0.5048$, $p < 0.1$) is statistically not significant.

These relationships can be interpreted in the following way: (1) In those insect–plant systems where one or two phytophagous species already reach a high average level of resource utilization (= systems with high intercepts), the effect of additional phytophagous species is relatively low (= systems with low slopes) and species numbers are a poor predictor of average resource utilization. (2) In insect–plant systems without clearly dominant phytophagous species (= low intercepts), the average level of resource exploitation increases with increasing values of species packing and the correlation between both parameters may be high; and (3) High values of resource utilization (attack of 90–100% of the flower head population) may be reached in systems with high species packing (*Centaurea solstitialis*) but also in systems with low species packing but highly dominant phytophagous insects (*Carduus nutans*, *Cirsium vulgare*, *C. heterophyllum*) (Fig. 1).

Table 1. Regressions of resource utilization on species packing (= S). n = number of flower head populations. Significance of the correlation coefficients: $^{+++}$ = $P = 0.001$, $^{++}$ = $P = 0.01$, $^{-}$ = $P = 0.1$. A′ = resource utilization for S = 1. B = slope. $\bar{y}$ = average resource utilization. (Samples without phytophagous insects have not been included in the regression.)

System	n	r^2	A'	B	$\bar{y}$
Centaurea solstitialis L.	55	0.847^{+++}	4.5%	8.46	35.9%
C. scabiosa L.	60	0.562^{+++}	14.9%	13.81	32.0%
C. diffusa Lam.	63	0.387^{+++}	3.6%	3.94	8.6%
C. jacea L.	50	0.279^{+++}	16.3%	9.96	30.0%
C. maculosa Lam.	51	0.248^{+++}	17.8%	6.87	32.5%
Carduus nutans L.	48	0.311^{+++}	36.2%	9.46	54.6%
Carlina vulgaris L.	35	0.264^{++}	12.9%	12.11	18.7%
Cirsium arvense (L.) Scop.	36	0.334^{+++}	14.4%	13.60	24.3%
Cirsium heterophyllum (L.) Hill	74	0.092^{++}	39.4%	8.25	52.2%
C. oleraceum (L.) Scop.	30	0.087^{-}	37.8%	4.34	46.6%
C. vulgare (Savi) Ten.	94	0.178^{-}	35.6%	4.18	40.9%

Geographic Differences

In some insect–plant systems the prediction of the average resource utilization on the basis of species packing becomes more precise, if correlations are calculated separately for the main collection areas (Fig. 2). In *Centaurea solstitialis* the hypothesis that there is a common slope in the resource utilization–species packing regressions has to be rejected, but it cannot be rejected in the other species represented in Fig. 2. Statistically significant geographic differences in resource utilization levels occur in *Centaurea solstitialis*, *C. scabiosa*, *Cirsium arvense* and *Carduus nutans*, but not in *Centaurea diffusa* and *C. maculosa*.

Table 2 gives the coefficients of determination obtained in stepwise multiple regressions, where the variables ‘species packing’ and a geographic factor (‘region’) were used to explain the variations of the variable ‘resource utilization’. (The variable ‘region’ is the rank if regions are arranged according to increasing average resource utilization.) With the exception of *Centaurea diffusa* there is a statistically significant increase in the coefficient of determination if both variables are entered into the regression.

There are many possible causes for geographic differences in the levels of resource utilization by the phytophagous guilds of Cynareae flower heads. Differences in climates and habitats or in the stability and abundance of the host plant populations may be involved. In allochthonous insect-host systems; i.e. in situations where both the host plant and phytophagous species are introduced into another continent (e.g. in cases of successful biological control), absence of parasitoids and predators of the phytophagous species is certainly one of the reasons of an increased exploitation of the host plant. In autochthonous insect-host systems, both species packing and resource utilization can be a function of the evolutionary age (Price 1983) and of the biogeographic history of the insect–plant system. Sobhian and Zwölfer (1985) have shown this for *Centaurea solstitialis*, where the number of phytophagous species and the consumption rates of flower heads significantly increase from the western to the eastern Mediterranean.

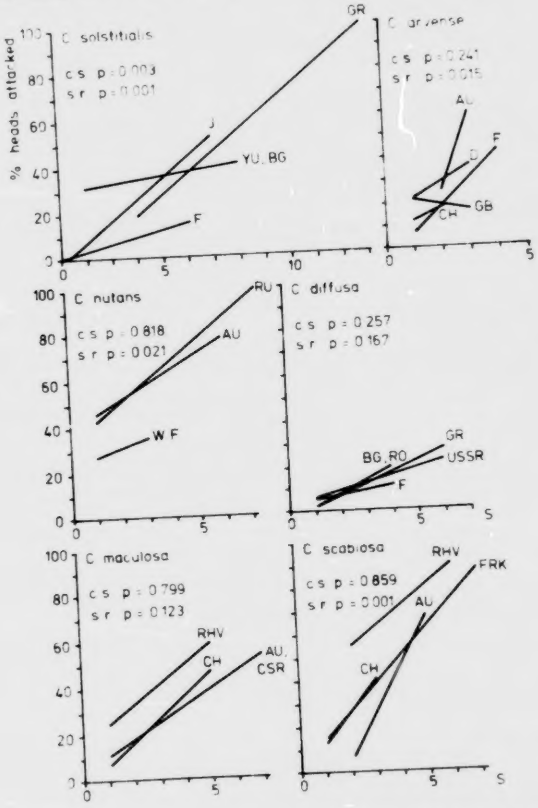

Fig. 2. Regressions of resource utilization on species packing calculated separately for geographic regions. c.s. = test for common slope (= O-hypothesis); s.r. = test for single regressions (O-hypothesis = no difference between regions); S = species packing; AU = eastern Austria; BG = Bulgaria; CH = Switzerland; CSR = western Slovakia; D = western Germany; F = France; FRK = Frankonia (w. Germany); GB = southern England; GR = Greece; I = southern Italy; RHV = Upper Rhine valley; RO = Rumania; USSR = Crimea, Caucasus; YU = Yugoslavia.

Taxonomic Isolation of the Host Plant

In contrast to Lawton and Schröder (1978), who could not show that 'taxonomic isolation' of Cynareae host species had a negative influence on insect species richness, Zwölfer (1982) demonstrated that there exists a statistically significant correlation between 'taxonomic isolation' (measured as the number of congeners of the Cynareae host) and 'species packing' (measured as the average number of phytophagous insects in a flower head population). Cynareae species in large genera tend to be exploited by more phytophagous species. The background of this phenomenon is discussed by Lawton and Price (1979). It can be explained by the fact that large Cynareae genera such as *Centaurea* or *Cirsium* have a broader pool of phytophages which facilitates host shifts and speciation. The level of 'species packing' obviously results from a stepwise recruitment of more or less specialized phytophagous insects, and this process requires both evolutionary time (Price 1983) and a reservoir of species predisposed to become associated with the plant. It is therefore plausible that species packing and usually also the level of resource exploitation is relatively low in Cynareae species belonging to small genera. As an example I have included *Carlina vulgaris* into my synopsis (Fig. 1). In Europe there exist only 12 species in this genus (as compared to 221 spp. in *Centaurea*, 60 spp. in *Cirsium*, 48 spp. in *Carduus*) (numbers from Tutin 1976). Cynareae species such as *Xeranthemum annuum* L. (3 spp. in the genus), *Echinops sphaerocephalus* L. (11 spp. in the genus), *Arctium lappa* L. (5 spp. in the genus), *Stachelina dubia* L. (5 spp. in the genus), *Galactites tomentosa* (L.) Moench (2 spp. in the genus), or *Silybum marianum* (L.) Gaertner (2 spp. in the genus) are other examples for low degrees of species packing in taxonomically isolated host plants (Zwölfer, unpubl. data).

Table 2. Coefficients of determination of regressions of resource utilization on the 'geographic factor' (= region), on species packing (= S) and on both 'region' and 'S' (= region + S). The 'geographic factor' represents the rank if observation regions are arranged according to increasing levels of resource utilization. (+) = Introducing the variable 'region' in addition to the variable S yields a statistically significant increase of the correlation coefficient.

System	r^2 (Region)	r^2 (S)	r^2 (Region + S)
Centaurea maculosa Lam.	0.083	0.248	0.339 (+)
C. diffusa Lam.	0.072	0.387	0.387 (-)
C. jacea L.	0.171	0.279	0.463 (+)
C. scabiosa L.	0.291	0.562	0.606 (+)
C. solstitialis L.	0.704	0.847	0.879 (+)
Cirsium arvense (L.) Scop.	0.289	0.334	0.423 (+)

Guild Structure and Resource Utilization

Wherever the insect complexes in Cynareae flower heads have been studied in detail (e.g. Varley 1947; Mellini 1951*a*, *b*; Zwölfer 1965, 1979; Redfern 1968; Eschenbacher 1982; Romstöck 1982; Angermann 1984; Michaelis 1984; Sobhian and Zwölfer 1985), it has been found that coexisting phytophagous species differ in parts of their ecological niches. If coexisting species belong to different families or orders (e.g. tephritids of the genus *Urophora* [Diptera: Tephritidae], gall wasps of the genus *Isocolus* [Hymenoptera: Cynipidae], and weevils of the genus *Larinus* [Coleoptera: Curculionidae]), they are exposed to different sets of parasitoids; i.e. to different mortality factors (Zwölfer 1975). Niche diversification is further increased by differences in: larval feeding habits (e.g. feeding in the receptacle, the ovarioles and maturing achenes); host ranges (stenophagous and euryphagous species); voltinism (univoltine and plurivoltine species); degree of larval aggregation (gregarious and solitary species); hibernation sites (within the flower head or outside); and so on. Thus, even if 12 phytophagous species coexist in a flower head population, as is the case with *Centaurea solstitialis* in Greece (Sobhian and Zwölfer 1985), the single members of the guild can be distinguished by traits of their life history, trophic strategies and mortality factors.

As concerns resource utilization, the most important niche difference is obviously that between gall-formers and species which feed without inducing gall formation. Gall-formers channel additional assimilates into the flower heads which they occupy, even if they do not cause a distinct structural gall as is the case with *Tephritis* spp. (Diptera: Tephritidae) in *Cirsium* heads (Romstöck 1982). As a rule, gall-formers are highly specialized in host selection: they oviposit early and, as there is only a short span during which oviposition is possible, they are dependent on strict synchronization with their host plants. As gall-formers can adjust the supply of assimilates of an individual flower head to the number of larvae occupying this head (Michaelis 1984; Romstöck 1982), they usually do not suffer from intraspecific competition. Therefore, they can afford to live gregariously within the flower heads of their hosts. Thus, the trophic strategy of the great majority of gall-formers associated with Cynareae heads is that of an 'early aggregated attack'.

Studies on the energy flow in flower head systems of *Cirsium vulgare*, *C. heterophyllum*, *Centaurea scabiosa*, and *C. jacea* have shown that this 'early aggregated attack' by single gall-former species accounts for 76% of the energy removed by the phytophagous guild from the flower head systems and transformed into larval biomass. This figure rises to 95% if the joules invested in lignified gall tissues are also taken into consideration (Zwölfer 1985).

Gall-formers with 'early aggregated attack' are the dominant phytophagous species in *Carduus nutans* (*Urophora solstitialis* F., *Rhinocyllus conicus* Froel. [Coleoptera: Curculionidae]), *Cirsium oleracum* (*Tephritis conura* Loew, *C. heterophyllum* [*Tephritis* nr. *conura*]), and *C. vulgare* (*Urophora stylata* L.). These species are responsible for the fact that in the respective Cynareae hosts, high levels of resource utilization are already reached with low values of species packing (= high intercepts of regression lines in Fig. 1).

From Fig. 1 it is obvious that in guilds with a dominant gall-former with 'early aggregated attack' the efficiency of additional species — usually solitary seed- and receptacle-feeders — tends to be lower and that the size of the guild tends to be smaller than if there are no dominant phytophages. The question arises: Which is cause and which is the consequence? Do dominant phytophagous species prevent other phytophages from reaching a higher efficiency? Or does a high degree of species packing prevent phytophagous species from becoming dominant? A definite answer must await the results of further analyses. The data presented here suggest for two reasons that the occurrence of dominant species may be rather a function of low species packing than a factor influencing it: (1) the regression of resource utilization on species packing of *Centaurea solstitialis* in the northern Balkan Peninsula (Fig. 2, 'BG,RO') demonstrates that there is a dominant phytophage. This is the tephritid *Urophora sirunaseva* (Her.) with a density of 37.2 ± 3.0 (mean and s.e., respectively) larvae/100 heads. *U. sirunaseva* is a gall-former with early and often aggregated attack, being comparable to the dominant *U. stylata* in *Cirsium vulgare* heads. *U. sirunaseva* also occurs in the Greek populations of *Centaurea solstitialis* with their unusually high degree of species packing (Fig. 2, 'GR'), but here it loses its dominant position (density 9.5 ± 3.6 larvae/100 heads) (Sobhian and Zwölfer 1985); and (2) So far the well documented cases of dominant phytophagous species reaching a high level of resource utilization in Cynareae heads refer to insect–plant associations in habitats of a post-Pleistocene age. This is particularly the case with *Cirsium heterophyllum* (Romstöck 1982), *Cirsium oleraceum* (Eschenbacher 1982), *Cirsium vulgare* (Redfern 1968; Michaelis 1984) and *Carduus nutans* and it has also to be assumed for the *Centaurea solstitialis* population in the northern Balkans. A span of less than 10,000 yrs may be enough for adapted phytophages to increase their specialization (Seitz and Komma 1984), but it is not sufficient for the accumulation of a large guild of phytophagous insects as occurred in the Greek populations of *C. solstitialis* occupying their sites for a much longer period.

Discussion

With regard to resource utilization, the insect communities in Cynareae flower heads can be arranged in three groups:

Group 1. Here, resource utilization as well as species packing is low (Fig. 3, lower third of the diagonally crosshatched area). Into this group fall host species which are taxonomically isolated (e.g. *Carlina vulgaris*) or allochthonous, geographically isolated host populations (e.g. west-European populations of *Centaurea diffusa*). Taxonomically isolated hosts are not (or only slightly) attacked by generalists and the specialized phytophages which we have observed so far on this type of host are mostly not very efficient as concerns resource utilization. Allochthonous host species, on the other hand, may be exploited by certain generalists but usually do lack specialists.

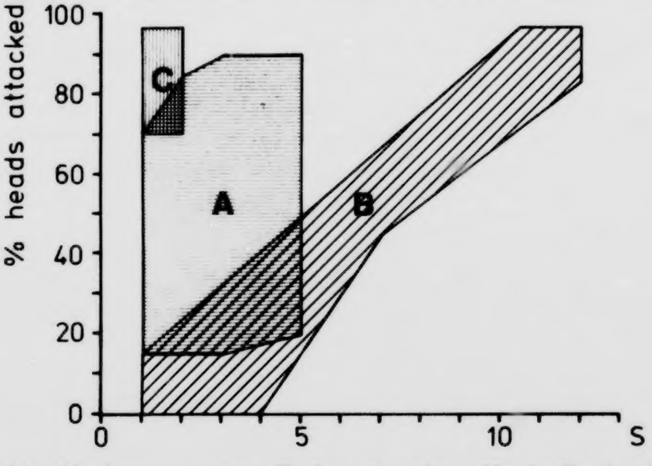

Fig. 3. Types of relationships between resource utilization and species packing (= S). A = Insect–plant systems with dominant phytophagous species. B = Insect–plant systems with correlations between resource utilization and species packing. C = Allochthonous insect–plant systems (successful biological control).

Group 2. In host species such as *Cirsium vulgare*, *C. oleraceum* or *C. heterophyllum*, resource utilization can be fairly high in spite of a low degree of species packing (Fig. 3, horizontally crosshatched area). The reason why these systems are undersaturated in species may be found in their post-Pleistocene origin; i.e. in an evolutionary relatively young age. The high level of resource utilization is mainly due to one or two phytophagous species belonging to a type which has also been successfully used in biological weed control. Such species form structural or physiological galls, attack the host in an early phase and usually exploit it gregariously.

Group 3. A high level of resource utilization has been reached in projects of biological weed control with one or two selected phytophagous species (Fig. 3, vertically crosshatched area). It also was found in the Greek populations of *Centaura solstitialis*; i.e. in an insect–plant system saturated in species (Fig. 3, upper third of the diagonally crosshatched area). In the case of biological control, well adapted phytophagous species can maximally exploit a host population, as they are not hindered by specialized natural enemies. In the case of east-Mediterranean *C. solstitialis* populations enough evolutionary time was available for the formation of a guild, the members of which fill almost all possible niches (Sobhian and Zwölfer 1985).

Efficient agents in the biological control of Cynareae (*R. conicus* against *Carduus nutans*, *U. stylata* against *Cirsium vulgare*, and *U. affinis* Frfld. against *Centaurea maculosa* and *C. diffusa*) commonly induce an additional supply of assimilates into the flower head and are fairly resistant against effects of interspecific competition. When used as biocontrol agents they may attack from 80–100% of the flower heads of a host population (Fig. 3). Harris (1980) and Myers and Harris (1980) have shown that in the case of *Centaurea maculosa* and *C. diffusa* heads, overall resource utilization is increased where two introduced species (*U. affinis* and *U. quadrifasciata* [Meig.]) exploit the same host population. This should encourage attempts in biocontrol projects to complement the effect of gall-formers of the type of 'early aggregated attack' by the introduction of selected seed feeders which exploit a later phase of the host and which are compatible with the gall-formers. Two problems are that such members of the phytophagous guilds of Cynareae heads are usually less specific, and that there are relatively few species suitable for biological control projects.

Our comparative study of insect complexes associated with European Cynareae hosts have shown that phytophages with 'early aggregated attack' only reach high levels of host utilization if they are genetically sufficiently adapted to a particular host species. In the weevil *R. conicus* this led to the evolution of host races (Zwölfer and Harris 1984) and in the tephritid *T. conura* to host races or sibling species (Seitz and Komma 1984). The geographic distribution patterns of these races and siblings suggest that this evolutionary process was slow and occurred only where abundant resources were available. Therefore the risk that introduced biocontrol agents would compromise the survival of endangered native North American *Cirsium* spp. seems negligible.

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Evaluating *Rhinocyllus conicus* (Coleoptera: Curculionidae) on *Silybum marianum* (Compositae) in Texas

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Abstract

The weevil, *Rhinocyllus conicus*, infested 48, 84 and 78% of the flowerheads of milk thistle, *Silybum marianum*, 3, 4 and 5 yrs respectively, after the original release was made in Central Texas. Egg to adult mortality was 71.7% with the greatest amount, 43.8%, occurring in the early instars. Weevils dispersed up to 5 km from the release site and reached densities of up to 27 larvae/head. The ovipositional period lasted 6 wks and was synchronized with development of terminal flowerheads but not with subterminals. The highest density of weevils was found in milk thistle plants growing in moist low areas, near trees and fencelines.

Évaluation de l'Efficacité de l'Agent Biologique *Rhinocyllus conicus* dans la Lutte Contre *Silybum marianum* au Texas

Le charançon *Rhinocyllus conicus* a infesté respectivement 48, 84 et 78% des capitules de chardon-Marie, *Silybum marianum*, 3, 4 et 5 ans après leur introduction à Marlin, au Texas. Au cours de la quatrième année, l'aire de dispersion des charançons s'était étendue sur 6,5 km au sud du site original d'introduction, mais n'a pas augmenté au cours de la cinquième année. Parmi les facteurs influant sur le développement des populations, mentionnons l'incapacité de la larve néonate à pénétrer l'épiderme des capitules, la courte période de floraison et le faible taux de ponte. La phénologie de la plante a également été étudiée.

Introduction

Rhinocyllus conicus Froelich (Coleoptera: Curculionidae) was first introduced from Europe into North America in 1968 for the biological control of several species of *Carduus* (Compositae) thistles and was widely credited with the successful reduction of thistle populations in several areas (Batra *et al.* 1981). A biotype of this weevil which appeared to prefer a closely related plant, milk thistle, *Silybum marianum* (L.) Gaertner (Compositae), was found in southern Italy by Goeden (1976). It was collected and released in California from 1971–74 (Goeden and Ricker 1977; Hawkes *et al.* 1972).

Milk thistle, a biennial or winter annual weed of Mediterranean origin, has become an increasingly obnoxious weed of winter pastures, disturbed and overgrazed rangeland, and wasteland of the southwestern United States (Correll and Johnston 1979; Parker 1972; Munz 1965). In Texas it was first reported growing in Sutton County in 1938 (Cory 1940) and is now a problem in many areas throughout the central region of the State. The weed competes with the more valuable grasses for water, space, and nutrients and grows in dense, compact stands which restrict cattle from parts of the pasture. The initial release of the weevil in Texas and some factors affecting its establishment on milk thistle are reported in this paper.

Materials and Methods

Approximately 800 overwintered adults of the univoltine *R. conicus* were collected from milk thistle in northern California by R.B. Hawkes and sent by air freight to Temple, Texas. Releases of 400 adults/site were made on 4 May 1978, in each of two pastures: Big Creek, located 8.1 km, and Reagan, located 19.3 km, southeast of Marlin, Texas (Falls County), along Texas Highway 6. Dense patches of milk thistles in the early flowering stage of development, occurred at both release sites, and were widely distributed in the area. Surveys to determine the percent infestation and distribution of the weevil were made on 21 May 1981, 2 June 1982, and 26 May 1983, at the original release sites and along transects of up to 15 km radiating out in the four cardinal directions from the release sites. The exact sampling locations were determined by the presence of the thistles and sometimes varied between years.

In 1981 and 1982, 25 central or lateral terminal heads were removed without bias from each site and dissected to determine the percent infestation and total mortality of the late larval and pupal stages. In 1983, 10 plants were removed without bias and the percent infestation and late larval and pupal mortality were determined for central terminal, lateral terminal, and sublateral heads. Density of milk thistle plants in the 2 ha pasture at the Big Creek release site was determined on 1 June 1983, by counting the number of plants of all sizes present, in 25 randomly selected 1 m^2 quadrats in each of two 200 m long transects laid parallel across the field.

In 1983, plants were sampled periodically throughout the immature life cycle of the weevil to determine the percent infestation, duration of oviposition, and density and mortality of each developmental stage in the central terminal, lateral terminal, and sublateral flowerheads. The number of eggs on the head was counted and 100 eggs were held to determine percent eclosion. Percent early larval mortality was determined by dividing the number of larvae found in the head by the number of entrance holes in the bracts and subtracting from 100. Percent late larval, pupal, and teneral adult mortalities were determined by dividing the number of dead individuals of each stage by the total number of individuals in each stage times 100.

Temperature and precipitation data from the Waco, Texas, meteorological station 35 km northwest of the site were used (Anon. 1983).

Results and Discussion

Recovery and Establishment

On 7 May 1981, three years after the initial release, numerous eggs and larvae and five adults were found on *c.* 200 milk thistle plants at the Big Creek release site. Two weeks later, 48% of 25 dissected heads from Big Creek were found to be infested with an average of 0.8 larvae/head (Table 1). Dissections of thistle heads from nearby areas indicated that the weevils had dispersed 0.5–3.0 km from the release site, although areas up to 10 km away were searched.

Number and density of weevils sharply increased at Big Creek in 1982. At the release site, 84% of 25 heads were infested with 4.7 larvae/head. Dispersal also increased and weevils were found as far as 6.3 km east and 3.0 km west of Big Creek.

No weevils were found at the second release site at Reagan nor in the immediate vicinity of this site despite several visits to the area in 1981–83.

In 1983 all heads on 10 plants sampled at each location were dissected. The number of weevils and percent of infestation at the release site continued to increase in the central terminal and lateral terminal heads at Big Creek (Table 2). The density and mortality of weevils found in the sublateral heads cannot be compared because they were not sampled in 1981 and 1982, but percent infestation and number of larvae/head were less than in the terminal heads, while mortality was higher. Sublateral head diameter of 1.37±0.49 cm was significantly less than the 3.[illegible]±0.23 and 2.34±0.55 cm diameter of the central and lateral terminal heads (Table 2), respectively, and may not have been suitable for oviposition (Zwölfer and Harris 1984) or larval development. Terminal heads were more susceptible to infestation than sublateral heads because they were present at the time the weevils were ovipositing, and the sublaterals appear later after oviposition has substantially decreased. Over 80% of the terminal heads were infested at the release site, 0.2 km north and 0.2 km west of the site. Weevils were present 5 km west of the release site but only one of 10 central terminal heads were infested. Weevils were not found 6.5 km east of the release site as they were in 1982.

Table 1. Number and percent infestation of *Rhinocyllus conicus* Froelich in terminal milk thistle (*Silybum marianum* L.) flowerheads at Big Creek site, Marlin, Texas, 1981–82.

Location[1]		1981		1982	
		No. of *R. conicus*/ infested head[2]	% heads infested	No. of *R. conicus*/ infested head[2]	% heads infested
Release site		0.82±1.15	48	4.67±3.62	84
North	0.2	1.00±0.00	16	3.61±2.57	72
	0.5	1.00±0.00	20	2.83±2.46	72
	1.0	—[3]	—	0.00±0.00	0
West	0.2	1.14±0.38	32	3.11±2.40	76
	2.0	0.00±0.00	0	0.00±0.00	0
	3.0	—[3]	—	1.00±0.00	8
South	0.2	2.18±1.72	42	2.75±1.71	20
	2.0	1.00±0.00	8	2.50±1.29	16
East	0.2	0.00±0.00	0	2.00±0.00	4
	0.5	1.33±0.58	12	0.00±0.00	0
	6.5	—[3]	—	2.00±1.41	8

[1] Direction and distance (km) from release site.
[2] Mean ± standard deviation of 25 heads/site/yr.
[3] Location was not sampled.

Overall, the population density increased to the north and west of the release site but decreased to the south and east. The highest density of weevils were observed in moist low areas, near trees and along fence lines while few or no weevils were observed in plants on an open rangeland near the release site. Cattle in the same field as milk thistles may also reduce weevil populations. Although the population density increased at the release site and up to 5.0 km distant, the migration rate was less than the 6.0–9.0 km/yr as reported by Rees (1977) in Montana.

Mortality

Oviposition occurred in the field from mid-April to mid-May. Weevils laid eggs under caps of masticated food particles on all parts of the bracts and on the base of the receptacles but not on the stem. In Texas, 21.4% of 98 eggs observed in 1983 did not eclose. Some predation but no parasitism was observed. Some physical dislodgement

Table 2. Number and percent infestation of *Rhinocyllus conicus* Froelich in milk thistle (*Silybum marianum* L.) flowerheads at Big Creek site, Marlin, Texas, 1983.

Location[1]		Flowerhead types								
		Central Terminal			Lateral Terminal			Sublateral		
		No. of *R. conicus*/ infested heads[2]	% heads infested[3]	No. of heads	No. of *R. conicus*/ infested head[2]	% heads infested[3]	No. of heads	No. of *R. conicus*/ infested head[2]	% heads infested[3]	No. of heads
Release site		13.90 ± 17.17	82 (19)	10	8.73 ± 7.63	87 (16)	52	2.50 ± 3.00	66 (11)	30
North	0.2	11.80 ± 10.60	100 (8)	10	13.22 ± 12.0	95 (10)	58	9.53 ± 8.86	92 (16)	38
	1.0	4.11 ± 3.62	66 (8)	9	6.77 ± 4.49	9 (16)	30	3.75 ± 4.22	6 (22)	12
West	0.2	6.50 ± 5.28	90 (5)	10	7.48 ± 6.57	85 (3)	46	2.89 ± 4.99	33 (31)	27
	3.0	0	—	10	0.15 ± 0.62	9 (0)	45	0.06 ± 0.24	6 (0)	17
	5.0	0.10 ± 0.32	10 (0)	10	0.08 ± 0.40	4 (100)	25	0	--	10
South	1.0	0	—	10	0.15 ± 0.37	11 (1)	39	0.80 ± 1.08	40 (8)	15
	2.0	0.10 ± 0.32	10 (0)	10	1.04 ± 1.75	32 (24)	28	0	—	10
East	2.0	0.44 ± 0.88	22 (25)	9	0.21 ± 0.66	8 (60)	24	0.33 ± 0.71	11 (60)	9
	6.5	0	—	10	0	—	29	0	—	10

[1] Direction and distance (km) from release site.

[2] Mean and standard deviation.

[3] Values in parentheses are percent late larval and pupal mortality.

Table 3. Mortality of *Rhinocyllus conicus* Froelich in flowerheads of milk thistle (*Silybum marianum* L.).

Type of flowerhead	Early larva			Late larva			Pupa			Adult		
	No. entrance holes/head[1]	% mortality	No. of heads	No. sampled /head[1]	% mortality	No. of heads	No. sampled /head[1]	% mortality	No. of heads	No. sampled /head[1]	% mortality	No. of heads
Central terminal	1.87 ± 2.00	28.2	25	6.80 ± 6.53	19.7	10	5.84 ± 3.96	18.0	10	8.11 ± 9.58	9.6	10
Lateral terminal	2.52 ± 3.31	60.7	25	4.25 ± 3.71	14.3	52	3.34 ± 2.74	15.5	52	4.75 ± 3.63	5.0	47
Sublateral	1.40 ± 2.81	33.7	25	1.58 ± 3.00	11.3	30	0.07 ± 0.27	0	30	1.18 ± 1.39	25.6	33

[1] Mean ± S.D.

of egg caps was observed. Goeden and Ricker (1980) reported no mortality from dislodging.

Newly eclosed larvae tunnelled through the bracts into the receptacle where they fed on the receptacle and the immature achenes. Number of larval entrance holes/head was used as an estimate of the number of successfully eclosed larvae. At Big Creek, number of entrance holes and percent early-instar mortality were highest in lateral terminal heads (Table 3). Mortality for 75 heads was 43.7% with an average of 1.92 entrance holes/head. Few dead larvae were found either in tunnels or receptacles. Occasionally, a small syrphid predator was found in a tunnel.

Late instar larvae and pupae usually were found around the edge of the receptacle. As density increased, more weevils were crowded to the center, although density was never so great as to force them into the peduncle as sometimes occurs on *Carduus* (Rees 1977). Damage was restricted to receptacles and achenes. Both density and mortality were highest in central terminal heads. Pupal mortality was significantly less in sublateral heads (where all four pupae recovered were alive) than in the central terminal or lateral terminal heads (Table 3). For 92 heads, there was an average of 3.8 late instar larvae/head with 15.6% mortality and 2.6 pupae/head with 15.8% mortality. No parasitism was observed in either larvae or pupae as compared with Europe, where weevil larvae in *Carduus* were heavily parasitized (Zwölfer and Harris 1984).

Table 4. Mortality of *Rhinocyllus conicus* Froelich/100 eggs on milk thistle (*Silybum marianum* L.), Marlin, Texas.

Stage	No. entering stage	% mortality during stage
Egg	100	21.4
Larva, early	78.6	43.8
Larva, late	44.2	15.6
Pupa	37.3	15.9
Adult, teneral	31.2	9.2
Adult, diapause	28.3	

Of the 2.94 teneral adults/head dissected from 90 mature brown heads in June 1983, 9.16% were dead from unknown causes. Greatest mortality was among adults in sublateral heads. The maximum daily mean air temperature of 29.1°C (Anon. 1983) probably did not produce temperatures in the head of 52–57°C which are necessary to kill *R. conicus* (Goeden and Ricker 1980), but the weevil may have been stressed by the combination of temperature and lack of plant moisture (Zwölfer and Harris 1984; Dowd and Kok 1983).

Mortality from eggs to adult in the life cycle of *R. conicus* was estimated at 71.7% (Table 4). This mortality was greater than the mean 55.8±20.0% calculated from data on milk thistle in California presented by Goeden and Ricker (1980). Thus for every 100 eggs oviposited on milk thistle heads, 28.3 adults were calculated to survive to mid-summer. Assuming that 50% of the adults are females and lay *c.* 200 eggs each (Phillips 1982), the weevil population should continue to increase. Neither life table measures adult survival during diapause which could affect the number of ovipositing females the following year.

Conclusions

Infestation rates of up to 27 larvae/individual head and a relatively low mortality rate of 71.7%, resulted in a substantial amount of damage to many heads. Nevertheless, damage was seldom complete and some undamaged, fully formed, and apparently viable achenes continued to be produced each year. In California, Goeden (1978) also found that even at the highest density achieved of 44 weevils/head total seed destruction did not result. Although *R. conicus* has been established for only five years in Texas, several factors were observed which may limit the weevil from achieving the degree of successful control reported in Virginia (Surles *et al.* 1974) and Montana (Rees 1977): (1) A short ovipositional period of 6 wks as compared with a period of 11 wks on *Carduus* in Europe (Zwölfer and Harris 1984). Oviposition was well synchronized with the development of the terminal flowerheads but was nearly completed by the time the sublateral heads appeared. (2) Larval densities observed in the field were insufficient to consistently destroy all or most of the achenes produced, even in terminal heads. Milk thistle heads required proportionally more larvae than the smaller *Carduus* heads, to achieve the same amount of damage. (3) *R. conicus* preferred plants growing in moist areas, near trees or along fence lines. They avoided plants in open flat rangeland even near the release site. This may be due to climatic stress of high air temperatures with insufficient plant moisture.

R. conicus is not a completely successful biological control agent. The weevil is capable of causing a significant amount of damage to milk thistle flowerheads but does not appear to be reducing the population density.

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Biological Control of Spotted Knapweed (*Centaurea maculosa*) — Host Range of *Puccinia centaureae*[*]

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Abstract

Spotted knapweed is a noxious introduced weed of pastures and rangeland of western North America. The weed is native to Eurasia where it has been reported to be attacked by autoecious *Puccinia* rust fungi. A survey for and collection of rust fungi attacking spotted knapweed were conducted in eastern and central Europe during the summer of 1982. Rust collections from Romania, Hungary, Austria, France and Germany were sent to the plant quarantine facility of Macdonald College of McGill University. Experiments were conducted in controlled-environment cabinets to evaluate the potential of the rusts as possible biocontrol agents of spotted knapweed. Many of the rust collections were virulent on North American populations of spotted knapweed. The host range of one virulent isolate, collected in Romania and identified as *Puccinia centaureae*, was confined to members of the sub-tribe Centaurineae in the Cynarae tribe of Asteraceae family. The rust was pathogenic on 26 species of *Centaurea* and three related species: *Amberboa moschata, Carthamus tinctorius* and *Cnicus benedictus*. Inoculations on several safflower cultivars have revealed that different levels of resistance to the rust isolate exist in this cultivated species.

La Lutte Biologique Contre la Centaurée Maculée (*Centaurea maculosa*) — Étude de la Spécificité de *Puccinia centaureae*

La centaurée maculée est une plante nuisible introduite qui a envahi les pâturages et prairies de la partie ouest du continent nord-américain. Cette plante nuisible est originaire d'Eurasie. Selon certains documents elle est la proie des rouilles autoïques du genre *Puccinia*. Un relevé et un échantillonnage de rouilles s'attaquant à la centaurée maculée ont été effectués en Europe centrale et en Europe de l'Est au cours de l'été 1982. Des échantillons de rouilles provenant de Roumanie, de Hongrie, d'Autriche, de France et d'Allemagne ont été envoyés au centre de quarantaine du Collège Macdonald de l'Université McGill. Au moyen d'essais en enciente climatisée, on a évalué les possibilités d'utilisation de ces rouilles comme agents de lutte biologique contre la centaurée maculée. Plusieurs de ces échantillons de rouille se sont avérés virulents sur les populations nord-américaines de centaurée maculée. L'étude de spécificité de l'un de ces échantillons provenant de Roumanie et identifié comme étant *Puccinia centaureae* a révélé que cette rouille ne s'attaque qu'à certaines plantes de la sous-tribu Centaurineae de la tribu des Cynareae (Asteracées). La rouille est pathogénique sur 26 espèces de *Centaurea* ainsi que sur trois autres espèces apparentées: *Amberboa moschata, Carthamus tinctorius*, et *Cnicus benedictus*. Des inoculations sur plusieurs cultivars de carthame (*C. tinctorius*) ont permis de déceler plusieurs niveaux de résistance à la rouille.

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[*] Manuscripts in preparation for publication elsewhere.

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Stress Inflicted by Organisms on Canada Thistle

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Abstract

The emphasis in biological weed control programs has been on weed suitability for biocontrol and host-specificity of selected organisms. Information on effects of damage caused to individual plants and on weed population dynamics has been limited. This case study with Canada thistle (*Cirsium arvense*) evaluated the stress inflicted by five organisms. Attack by the seed head predator, *Orellia ruficauda*, occurred in up to 70% of the heads and caused about 21.5% seed reduction/head and may reduce seed dispersal. Root crown damage caused by *Cleonus piger* sometimes resulted in plant death, but regeneration of damaged vascular tissue also occurred. A defoliation level of > 50% was required to reduce thistle vigour and *Cassida rubiginosa* rarely achieved this in nature. *Urophora cardui* gall formation on the mainshoot resulted in stunted plants and reduced flowering. Plants that emerged systemically infected with the rust, *Puccinia punctiformis*, rarely survived the season.

Effets Perturbateurs des Organismes sur le Chardon des Champs

Dans les programmes de lutte biologique contre les plantes nuisibles, la priorité a été accordée à l'aptitude des plantes nuisibles à se soumettre à un contrôle biologique et à la spécificité d'hôtes d'organismes choisis. Les données sur les effets des perturbations causées à chaque plante et sur la dynamique des populations des plantes nuisibles sont limitées. Cette étude de cas sur le chardon des champs (*Cirsium arvense*) avait comme objectif d'évaluer les effets perturbateurs causés par cinq organismes. L'attaque du prédateur des têtes de graines, *Orellia ruficauda* a été relevée dans 70% des capitules où elle a entraîné une réduction d'environ 21,5% du nombre de graines par capitule et elle peut entraver la dispersion des graines. Dans certains cas, la détérioration des couronnes de racines due à *Cleonus piger* a provoqué la mort des plants; mais on a également constaté la régénération des tissus vasculaires ravagés. Une défoliation de l'ordre de plus de 50% était nécessaire afin de réduire la vigueur des chardons, ce que *Cassida rubiginosa* a rarement pu provoquer dans la nature. Des plants rabougris et une diminution de la floraison ont été causés par la formation de galles de *Urophora cardui* sur la pousse principale. Les plants qui étaient systémiquement infectés par *Puccinia punctiformis* (rouille) au moment de leur apparition, résistaient rarement pendant la saison.

Introduction

It has been recognized in the last decade that a major constraint to biological weed control programs is lack of information on stress of target weeds resulting from attack of organisms employed (Harris 1978, 1980). For the purpose of this study, stress is defined as a measurable adaptation or response to some perturbation in the environment. A negative response could potentially result in reduction of reproductive capacity, and therefore could affect the population dynamics of the weed. Plant abundance depends on several factors and the interactions and relationships can be very complex. Factors which can determine whether or not an agent will reduce plant populations include: climatic and edaphic conditions; intra- and inter-specific competition (both agent and weed levels); and characteristics of the biocontrol agent such as searching efficiency, rate of increase, ease of establishment, and predation (Harris 1980; Winder and van Emden 1981).

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Stress should be considered as a selection criteria for biological control candidates. One proposal is to determine the type of damage caused and relate this to an effectiveness scale. This idea has merit, but there is little agreement as to what type of damage is most effective and it is likely that standards could not be developed since the stress is probably dependent on unique characteristics of the agent and the target weed. Harris (1980) proposed several possible techniques to increase stress including: (a) decrease the mortality of the agent; (b) increase the fecundity of the agent; (c) increase the number of agent species on any target weed; (d) alter cultural practices to stress weed while still favouring the agent; and (e) select agents that inflict a high stress load.

Perhaps future biological control programs would benefit from a procedure based on a variation on a theme from Greek mythology as follows: (1) Know the plant — understand the population dynamics, habitats, growth habits, vulnerable parts of the life cycle, and so forth, of the target weed; (2) Know the agent — understand the phenology of the agent relative to the plant, the number of generations, level of field attack; and (3) integrate this knowledge of host and agent and determine the level of stress caused by the organisms and relate this to a stress threshold arrived at through simulation or modelling techniques using the population dynamics of the host.

Most of the work in biocontrol is directed towards vigorous and troublesome perennial weeds and the emphasis of herbivory is centered on annual production of seed or biomass rather than the often more important vegetative propagation from root buds or rhizomes. These asexual propagation methods of perennial weeds present a more complex control problem than for an annual weed or a biennial weed. Vegetative propagation also increases the complexity of studying stress effects and population dynamics of the perennial weeds.

A case study involving the stress caused by five natural enemies on Canada thistle (*Cirsium arvense* [L.] Scop.; Compositae) will be discussed (Forsyth 1984). The natural enemies include: *Orellia ruficauda* (F.) (Diptera: Tephritidae), a seed feeder; *Cleonus piger* Scop. (Coleoptera: Curculionidae), a root crown inhabitant; *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae), a defoliator; *Urophora cardui* (L.) (Diptera: Tephritidae), a stem gall causer; and *Puccinia punctiformis* (Str.) Rohl (Uredinales), a systemic rust.

In this discussion, the following points of stress physiology will be addressed:

(1) Importance of feeding loci for biocontrol of perennials:
    (a) seed predator (loss of reproductive capacity — seed);
    (b) root crown inhabitant (blockage or damage to translocation elements);
    (c) defoliator (loss of photosynthetic area);
    (d) gall formation (alteration of resource partitioning); and
    (e) systemic rust growth (disease);
(2) Plant phenological stage of attack;
(3) Density of natural enemies/amount of damage;
(4) Length or repetitiveness of attack; and
(5) Combination of stresses.

Materials and Methods

These studies were performed from 1980–83 at Macdonald College of McGill University, Ste.-Anne-de-Bellevue, Quebec, Canada. Field studies were done on the five natural enemies at four field sites on the College property. Physical damage caused by the agents was qualitatively assessed by light microscopy. Quantitative data on stress was gathered for gall formation, after rust inoculations with urediniospores, for insect and simulation defoliation and simulation of root crown damage. Parameters recorded included height, dry weight, root, bud and ramet production, among others. Additional physiological measures including sugar and protein content of various tissues, radioactive tracer experiments and others were also performed. Manuscripts on the stress physiology caused by each of these organisms are in preparation for publication elsewhere.

Results and Discussion

Feeding Loci

Seed predation. O. ruficauda attacked up to 70% of seed heads and destroyed 0–90% of the seeds/head. The effect of this predispersal seed predator is probably minimal in reducing populations of established stands in pastures and rangelands where Canada thistle seedling survival is low. Seed predation is not as important in reducing a perennial weed population with alternate means of propagation as it is to an annual plant where seed production is the only means of propagation. However, if a seed predator does reduce the seed production of a perennial weed, it can potentially reduce the dispersal and thereby possibly decrease infiltration of arable land and minimize new stands initiated from seedling growth.

Root crown inhabitant. C. piger larvae caused a rudimentary gall to be formed in the root crown region of Canada thistle. Up to 27% of sampled plants contained *C. piger* larvae in Quebec, Canada, with wilting the field symptom of *C. piger* habitation. Microscopal examination indicated that *C. piger* causes wilt by damage to the xylem tissue. However, tissue regeneration occurred and only occasionally did attacked plants die. Plant death occurred primarily on poor soils. More commonly, attacked plants were not adversely affected, with flowering time and flower number not significantly reduced. The weevil tended to choose larger plants (due most likely to its large size). The effect of *C. piger* on ramet or root bud production is not known.

Defoliation. In the field, *C. rubiginosa* caused minimal damage to Canada thistle plants, and as with *C. piger*, seemed to be attracted to larger plants. Simulation experiments indicated that maximum stress occurred on young plants when the defoliation level was high (50% leaf removal or more). High levels of defoliation can significantly reduce height, flower number, sideshoot number and dry weights of the defoliated plant, root and total dry weight, and most importantly for future control, a reduction of root bud and ramet production.

Gall formation. U. cardui, an insect imported into North America in the classical biological control program for Canada thistle, induces stem gall formation on the sideshoots and/or mainshoot of Canada thistle plants. For current year production of biomass, mainshoot galls are much more detrimental to the plant than sideshoot gall development, resulting in lower heights and reduced and delayed flowering. Gall formation can also significantly reduce root dry weight and ramet number. Radioactive tracer studies indicated that the gall was a weak physiological sink when it was forming, but not when mature. Sideshoot galls appeared to have less effect than mainshoot galls on current year production, but effect on root bud production is not known. Most of the work presented was conducted under controlled environmental conditions and the effect in nature could be either less detrimental, due to a more advanced and complex root system with greater resource storing capabilities, or more detrimental due to additional environmental stresses, such as other natural enemies and competition from other plants.

Systemic rust formation. *P. punctiformis* can significantly stress Canada thistle (Watson and Keogh 1981). Systemically infected shoots rarely survive the season, but the naturally occurring field level is low and rarely eliminates a Canada thistle population. As early as 1915, Cockayne (1915) recommended that infection with this rust must be increased beyond naturally occurring levels to be an effective means of control. Some progress was made on the examination of the infection process. Under controlled environmental conditions, it was found that as number of leaves infected by inoculation with urediniospores increased, proportion of systemic infection increased. With multiple inoculations, more frequent inoculations resulted in earlier, greater number and greater frequency of production of systemically infected ramets. Some preliminary tissue culture work indicated that systemically infected callus could be prepared.

Summary. There appears to be no magical place to attack a perennial weed. Consideration of the type of attack should not become a prerequisite for agent selection, but rather the damage should result in a reduction of reproductive capabilities. Actual damage (type and/or amount) is not important, but stress on root bud and seed production is important. No firm conclusions as to which type of damage would be most effective can be stated from this study. The efficacy of a seed head predator seems relatively low for Canada thistle. It seems reasonable to assume that an additional seed head predator in eastern Canada would not be an asset. However, in western Canada, where Canada thistle is a problem in cultivated fields, additional seed feeding may be appropriate. Some predation by ***Rhinocyllus conicus*** Froelich (Coleoptera: Curculionidae), a biocontrol agent released on *Carduus nutans* L. (Compositae) does occur, but the effectiveness on Canada thistle is not known.

Damage to vascular tissue seemed to be effective if the root system was already under stress; the only field plants that died from *C. piger* attack occurred on very poor soil. The tremendous regenerative capacity of the vascular system counteracts the damage and probably also the disorganization caused by gall formation.

U. cardui gall formation resulted in only a low level of stress to the plant. *U. cardui* galls are weak sinks. This, however, does not preclude all gall inducers which may be more efficient at assimulate repartitioning during their formation. If a gall were a good sink, then it could draw resources from the roots and thereby reduce vegetative propagation.

For perennials, defoliators must remove a substantial amount of foliage to have a detrimental effect. Leaf regrowth capacities are substantial and only defoliation levels of greater than 50% resulted in any significant damage.

The systemic rust was the most effective natural enemy in this study. Further studies for the determination of techniques needed to cause an epidemic of this pathogen should be initiated.

Phenology Stage of Weed at time of Attack

There have been suggestions that an effective perturbation should occur when the carbohydrate level is low. For gall formation, and in defoliation simulation experiments, stress on regenerative factors (root weight, root bud number) was greater for young plants (Table 1). For biocontrol of perennial weeds, it may be more effective to attack younger plants to decrease initiation of root bud primordia rather than delaying until later in the season when root buds are already formed. Both *U. cardui* and *C. rubiginosa* attack plants during early bud to flowering stages and are therefore poorly synchronized with their host plant in inflicting damage. A practice such as early mowing or sheep grazing could stunt plant development to allow for better synchrony of these two organisms and possibly greater stress. The rust illustrates the effectiveness of early attack on the weed; each plant that emerges in the spring infected with the rust usually dies.

Density of Natural Enemy or Degree of Damage

It seems reasonable to assume that the greater the damage (or the higher the number of the natural enemy), the more detrimental the effect on the plant. This assumption was confirmed by this study with both the gall inducer and defoliation simulation. Gall size was positively correlated with larval number, and it has been postulated that stress on the plant should increase with larvae number. Evidence of this was indicated in Table 2. Higher levels of defoliation resulted in greater stress on plants (Table 3). The threshold concept of biological control assumes that a damage level can be achieved above the threshold and result in plant population reductions. However, no proof that the carrying capacity of the agents will correlate with the threshold level is manifest; this remains to be tested.

Table 1. Effect of defoliation[1] and age of plant at time of defoliation on plant growth and reproductive parameters.

Age[2]	Height (cm)		Ramet no.		Flower no.		Root bud no.		Dry weight (g)			
									Plant		Root	
	S[3]	R[3]	S	R	S	R	S	R	S	R	S	R
5	59.9*a*[4]	39.9*b*	9.4	6.4*c*	4.4	0.8*b*	12.3	8.4	7.0*a*	4.4*a*	4.7	3.9*b*
10	56.8*ab*	40.6*b*	11.5	7.4*bc*	3.5	1.1*b*	14.6	9.4	7.0*a*	4.4*a*	4.8	4.5*ab*
15	52.8*b*	45.2*ab*	10.1	9.5*ab*	3.6	1.3*b*	13.0	11.6	5.8*a*	4.8*a*	4.7	4.8*a*
20	51.8*b*	50.8*a*	8.0	10.4*a*	4.1	2.3*a*	9.9	12.4	5.2*b*	5.1*a*	4.3	4.0*b*

[1] Averaged over five defoliation levels: 0, 25, 50, 75 and 100% of leaves removed.

[2] Age in leaf number at first treatment.

[3] Treatments: S = single defoliation; R = repeated defoliation.

[4] Means with the same letter in the same column are not significantly different. Means with no letters are not significantly different. (Duncan's multiple range test, $P < 0.05$.)

Length and/or Repetitiveness of Attack

The longer the plant is under stress, the greater will be the detrimental effects. Also, if the duration is short, then repetition of perturbation could be more detrimental than a single one (Winder and van Emden 1981). This was found for defoliation simulation in this study (Tables 1 and 3). The repeated defoliation treatment generally resulted in lower vigour than a single defoliation. This factor is complexed by the time of initiation of herbivory or times of repeated attack, length of time between attacks (time for compensatory growth), number of attacks, or length of a single long attack. Repeated inoculations with *P. punctiformis* also resulted in a greater production of systemically infected ramets.

Combinations

Although spectacular success in biological control has been achieved with only one agent/weed (for example, *Cactoblastis cactorum* Berg [Lepidoptera: Pyralidae] moth on prickly pears, *Chrysolina* spp. [Coleoptera: Chrysomelidae] beetles on St. John's wort and *R. conicus* on nodding thistle), these cases are exceptional. Most weeds probably require three or more natural enemies to achieve control. A mathematical model based on the Leslie matrix model, used to test effects of various natural enemies, indicated that separately the organisms did not reduce the weed, but in combination, the effect was much greater. Without these natural enemies, Canada thistle could be a greater problem than it is at present; indeed in the western Canadian provinces where *C. rubiginosa* and *C. piger* do not occur and *P. punctiformis* is rare, Canada thistle is a greater problem. This indicates that the stress resulting from attack by these organisms, though minor, is probably affecting Canada thistle population dynamics.

Table 2. Effect of gall size on growth and reproductive parameters of Canada thistle (*Cirsium arvense* L.).

Parameter	Gall size[1]			LSD
	Small	Medium	Large	(0.05)
Height (cm)	36.5	28.9	25.0	5.5
Root bud number	28.0	19.6	11.0	10.4
Fresh weight (g)				
Plant[2]	34.8	25.9	24.3	6.8
Root	19.3	11.7	15.5	3.4
Dry weight (g)				
Plant[2]	6.8	5.6	5.3	1.8
Root	4.2	2.8	3.6	1.0

[1] Size: small, < 5 cm^2; medium, 6–8.5 cm^2; and large, > 8.5 cm^2.

[2] Weight of remaining stem and leaves after gall removal.

Conclusions

Interactions of natural enemies and plant populations are complex and studies should become a part of the biological control program protocol and could eliminate further study on agents which either: (a) are inappropriately synchronized with the host plant phenology to cause significant damage; (b) do not cause a relatively high level of damage; or (c) cause damage to plant loci which are highly resistant to damage. These comments do not suggest that only those organisms that cause massive damage be considered, since each one no matter how small adds to the stress of the plant, but that more astute selections may be made. An understanding of the stress levels that each agent inflicts on the plant relative to known threshold stress levels, which can result in population decline would be the ideal situation, a concept which is being examined at present. This would allow prediction of the number of insects and pathogens required to obtain control. This study has shown that for perennial weeds, the most detrimental type of damage appears to be a virulent pathogen, which results in demise of each plant it infects, in root damage, and ultimately in reduction of vegetative propagation. Defoliation, if heavy and repetitive would be damaging, since it draws resource from the root and flowers for the replacement of the leaf material lost. Gall inducers, rated by Harris (1973) as causing low damage, do seem to have less detrimental effect, since as Shorthouse (pers. comm.) states, gall insects live 'off the interest', not 'off the capital'.

Little can be done to alter insect development rates to match the susceptible stage of the weed, but management practices to delay weed growth can be utilized. Appropriate timing of damage may be as important as massive damage.

This type of information may be important for the development of biocontrol programs and may provide more accurate prediction for agent selection. The tremendous regenerative capacity and vigour of perennial weeds makes them effective weeds and difficult to control. Many interacting factors act together to regulate the population dynamics of the weed. This study has begun the investigation of a relatively unknown area, the effect of the natural enemies on the weed. Present similar studies on another perennial weed problem, leafy spurge (*Euphorbia esula* L.; Euphorbiaceae) are in progress.

Table 3. Effect of defoliation level[1] on plant growth and reproductive parameters.

Defoliation percentage	Height (cm)		Ramet number		Flower number		Root bud number		Dry weight (g)			
									Plant		Root	
	S[2]	R[2]	S	R	S	R	S	R	S	R	S	R
0	60.1*a*[3]	58.3*a*	11.2	11.7*a*	6.1*a*	3.6*a*	13.0	11.7*ab*	7.4*a*	7.3*a*	5.3*a*	6.0*a*
25	51.7*b*	54.2*a*	10.0	9.4*a*	4.9*a*	1.2*b*	13.0	14.9*a*	6.4*ab*	5.8*b*	4.8*ab*	5.0*b*
50	58.4*a*	45.8*b*	8.6	9.9*a*	4.6*ab*	1.2*b*	12.4	9.6*b*	6.3*ab*	4.8*cb*	4.7*ab*	4.6*b*
75	49.4*c*	31.9*c*	11.0	6.2*b*	1.7*b*	0.4*b*	12.1	10.8*ab*	5.2*b*	3.0*d*	4.3*c*	3.2*c*
100	56.8*ab*	27.1*c*	8.0	4.8*b*	1.9*b*	0.5*b*	11.9	4.9*c*	6.0*b*	2.0*e*	4.1*c*	2.1*d*

[1] Averaged over four ages: 5, 10, 15, and 20 leaf stages.

[2] Treatments: S = single defoliation; R = repeated defoliation.

[3] Means with the same letter in the same column are not significantly different. Means with no letter are not significantly different. (Duncan's multiple range test; $P < 0.05$.)

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Biological Control of Musk Thistle by *Rhinocyllus conicus* (Coleoptera: Curculionidae) in Virginia from 1969 to 1980

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Abstract

Population dynamics of *Rhinocyllus conicus*, an introduced weevil, and its target weed, musk thistle, was studied in detail at two widely separated sites in Virginia over a span of 11 yrs. One site is located in Frederick County in northeast Virginia and the other is in Pulaski County in southwest Virginia. A similar pattern of insect increase followed by thistle decrease was observed in both sites. Thistle reduction was dramatic after the explosive phase of the weevil build-up during the fifth year after release. This was followed by weevil dispersal and resurgence of plant density. However, the resurgent plants were much smaller and produced fewer buds than the thistles prior to weevil release; thus bud density during resurgence was significantly lower than the initial density. Between 1969 and 1980, decline in musk thistle bud numbers was 80% at the Frederick County and 97% at the Pulaski County site.

Lutte Biologique Contre le Chardon Penché par *Rhinocyllus conicus* (Coleoptères: Curculionides) en Virginie, de 1969 à 1980

La dynamique des populations de *Rhinocyllus conicus*, un charançon introduit, et l'hôte cible, le chardon penché, ont fait l'objet d'études approfondies en deux emplacements de la Virginie fort éloignés pendant une période de 11 ans. Un des sites est situé dans le Frederick County dans le nord-est de la Virginie et l'autre, dans le Pulaski County dans le sud-ouest de la Virginie. Un modèle similaire d'augmentation des populations d'insectes suivie d'une diminution des chardons a été observé aux deux endroits. La réduction des chardons a été très marquée après la période de prolifération des charançons au cours de la cinquième année après la libération. Par la suite, les charançons se sont dispersés et il y a eu réapparition des plantes. Toutefois, les nouvelles plantes étaient beaucoup plus petites et produisaient moins de bourgeons qu'avant l'introduction des charançons; par conséquent, la densité des bourgeons au cours de la réapparition était notablement inférieure à la densité initiale. Entre 1969 et 1980, la réduction du nombre de bourgeons des chradons penchés était de 80% dans le Frederick County et de 97% dans le Pulaski County.

Introduction

Musk thistle (*Carduus nutans* L.; Compositae) is an introduced weed which has become a major problem in pastures and highway embankments in the U.S.A. since the early sixties. Based on specimens studied, McCarty (1978) indicated that the musk thistle species was *Carduus theormeri* Weinmann. The biological control of *Carduus* thistles in Virginia was initiated in 1969 with the introduction of *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae). Establishment of *R. conicus* at 12 sites was first reported by Surles *et al.* (1974); four of the successful establishments were on musk thistle. Subsequent reports by different workers of successful establishments of *R. conicus* in other States have led to much interest in the potential of this weevil in thistle suppression. Boldt and Kok (1982) summarized the bulk of the literature published on this weevil. Although numerous publications have documented various aspects of the biology, mortality factors, and impact of *R. conicus* on musk thistle, all of the reports have dealt with short-term studies of 3–6 yrs or less of thistle–weevil interactions. None discusses in detail the impact of the weevil on musk thistle over a longer term. This study examines in some detail the population dynamics of the weevil and thistle populations between 1969 and 1980 at two of the sites where *R. conicus* was first established in Virginia. One, located in Frederick County in northeastern Virginia, was predominantly of musk thistle, with some plumeless thistles (*C. acanthoides* L.); the other, located in Pulaski County in southwestern Virginia, was pure musk thistle. These were two of the four original establishments on musk thistle (Surles *et al.* 1974), and were selected because of the relatively unaltered land use throughout this period. The other two original establishments were not studied after 1976 because of cropping changes; one site was converted to an orchard after a dramatic decline in thistle population in 1976, and the other site was plowed and planted with crops after it had been left fallow for 6 yrs.

Methods and Materials

Site Description

Thistle plants were extensive throughout the immediate area and around the Frederick County site. The release area was an old pasture (*c.* 1000 m^2) which had not been used for a number of years at the time of release of *R. conicus*. It was occupied by thistles and a mixture of grasses. It is bordered to the northeast by forest; to the southwest and northwest by state road 671 and similar unused, weedy pasture; to the northeast by an alfalfa field, and a wooded area beyond this. One thousand *R. conicus* released at this site in September 1970 became established within 2 yrs.

The Pulaski County release site was very heavily infested with musk thistle. It is part of a large farm of over 1000 ha, mainly of open pasture, with trees on the western and northern perimeter, and ridges on the eastern and southern side. Although only 100 *R. conicus* were released at this site in June 1969, it became well established within 2 yrs.

Population Dynamics

Qualitative surveys were conducted in 1971 for the presence/absence of *R. conicus*, by random checks of thistles for eggs, larvae or adults. Quantitative surveys were conducted in June 1972 and in subsequent years through 1980 using the swath transect method as described by Kok and Surles (1975). One thousand plants (5 replicates of 200) were sampled by five individuals each year. Records of the following were kept for each plant examined: number of weevil eggs on the terminal and two most advanced lateral flower heads, abortion of the terminal or lateral heads, number of heads/plant, plant height, and number of adult weevils encountered on the plant. The total area surveyed was used to estimate density of plants in the site, and for calculation of changes in plant density for each year.

Results and Discussion

Both sites showed increases in weevil egg numbers within the first few years (Tables 1 and 2). The explosive phase of *R. conicus* multiplication occurs about 5 yrs after release (1974 for the June 1969 release in Pulaski County, and 1975 for the 1970 September release in Frederick County). Early establishment is important for this to occur. Although early spring release is much superior to late summer release (Kok 1974), and the September 1970 release at the Frederick County site was biologically two generations behind the June 1969 release at the Pulaski County site, this was partially offset by a 10-fold increase in numbers of weevils for the September release. Both sites were well established with *R. conicus* within 2 yrs. The explosive phase is indicated by not only the higher infestation rate of plants but also by a greater incidence of eggs on the lateral buds. The impact on thistle density is most apparent after this explosive phase of the weevil in terms of reduction of plant density, number of buds/plant, and plant height. Heavy infestations of both the terminal and lateral heads lead to a subsequent dramatic decline of thistle density in the next year. This significant plant reduction, however, does not remain constantly low, but tends to fluctuate. With reduction in plant density, dispersal of the weevil greatly increases as a function of host scarcity, resulting in a rebound in thistle population. Additionally, if the fields are cut as was the case at these two sites, the next 2 yrs revealed a resurgence of thistle density back to their original pre-release levels. The fields however, do not resemble the pre-release stage because of some fundamental changes in the plants. The resurgent plants are mainly single-bud plants less than a meter high, whereas the former multi-budded plants were taller, averaging 1.4 m or more. Many of these new low plants with tiny single buds escape infestation because the weevils are more attracted to larger plants. Thus, there is a significant drop in plants infested by the weevil in the year following wide dispersal of the weevil (Tables 1 and 2).

Table 1. Population dynamics of weevil–thistle in Frederick County, northeast Virginia[1].

Observation	Year – Means[2]								
	1972	1973	1974	1975	1976	1977↓	1978↓	1979	1980
Plant infestation (%)	26.7 *a*	49.9 *b*	50.8 *b*	74.3 *c*	50.0 *b*	70.0 *c*	77.6 *cd*	91.9 *d*	73.0 *c*
Terminal bud infestation (%)	26.7 *a*	42.8 *b*	47.6 *b*	73.7 *c*	48.2 *b*	67.6 *c*	77.3 *cd*	91.6 *d*	72.6 *c*
1st lateral bud infestation (%)	2.5 *a*	42.8 *b*	52.5 *bc*	75.4 *de*	60.8 *c*	75.4 *de*	74.4 *de*	90.5 *e*	62.1 *cd*
2nd lateral bud infestation (%)	2.5 *a*	43.6 *b*	54.8 *bc*	77.3 *de*	63.4 *cd*	62.8 *cd*	74.6 *de*	88.6 *e*	56.0 *bc*
No. eggs/terminal bud	1.2 *a*	3.1 *a*	3.2 *a*	7.2 *b*	6.4 *b*	7.5 *b*	8.2 *bc*	19.3 *d*	10.8 *c*
No. eggs/1st lateral bud	0.04*a*	2.4 *ab*	3.0 *b*	5.5 *bc*	6.4 *c*	6.0 *c*	5.8 *c*	14.2 *d*	7.9 *c*
No. eggs/2nd lateral bud	0.04*a*	2.7 *ab*	3.3 *bc*	5.7 *cd*	6.9 *d*	5.0 *bcd*	5.9 *d*	12.8 *e*	7.4 *d*
Aborted terminal buds (%)	0 *a*	0 *a*	1.6 *ab*	2.7 *bc*	1.3 *ab*	3.0 *bc*	9.2 *d*	2.7 *bc*	4.2 *c*
Aborted 1st lateral buds (%)	0 *a*	0 *a*	0 *a*	0 *a*	0 *a*	0 *a*	1.0 *a*	0.5 *a*	0.7 *a*
Aborted 2nd lateral buds (%)	0 *a*	0 *a*	0 *a*	0 *a*	0.4 *a*	0.9 *a*	2.0 *a*	0.3 *a*	0.3 *a*
No. buds/plant	4.2 *b*	2.5 *a*	2.2 *a*	2.1 *a*	2.1 *a*	2.2 *a*	2.8 *ab*	2.4 *a*	2.4 *a*
Thistle density (no./m^2)	0.36*c*	0.17*b*	0.15*ab*	0.13*ab*	0.06*ab*	0.04*a*	0.16*ab*	0.35*c*	0.11*ab*
Plant height (m)	1.4 *b*	0.8 *a*	0.8 *a*	0.8 *a*	0.7 *a*	0.7 *a*	0.9 *a*	0.9 *a*	0.9 *a*
No. adult weevils encountered (total)	2	9	28	102	25	35	217	98	25
No. buds/m^2	1.5 *c*	0.4 *ab*	0.3 *ab*	0.3 *ab*	0.1 *a*	0.1 *a*	0.4 *ab*	0.8 *bc*	0.3 *ab*
Bud reduction (%)	0 *a*	73.3 *c*	80.0 *cd*	80.0 *cd*	93.3 *d*	93.3 *d*	73.3 *c*	46.7 *b*	80.0 *cd*

[1] 1000 *R. conicus* released in September 1980; observations based on 1000 plants; arrow indicates year when pasture was mowed.

[2] Means followed by the same letter for each row are not significantly different ($P \leq 0.01$, Duncan's MRT).

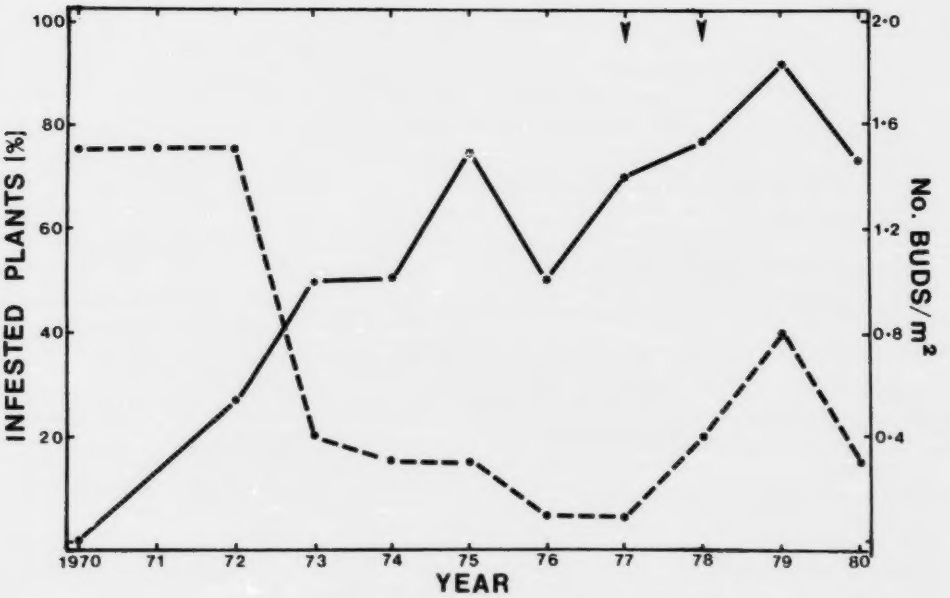

Fig. 1. Percent infested plants (*) and no. buds/m² (●) in Frederick County site, Virginia, from 1970–80; field mowed during year (▼).

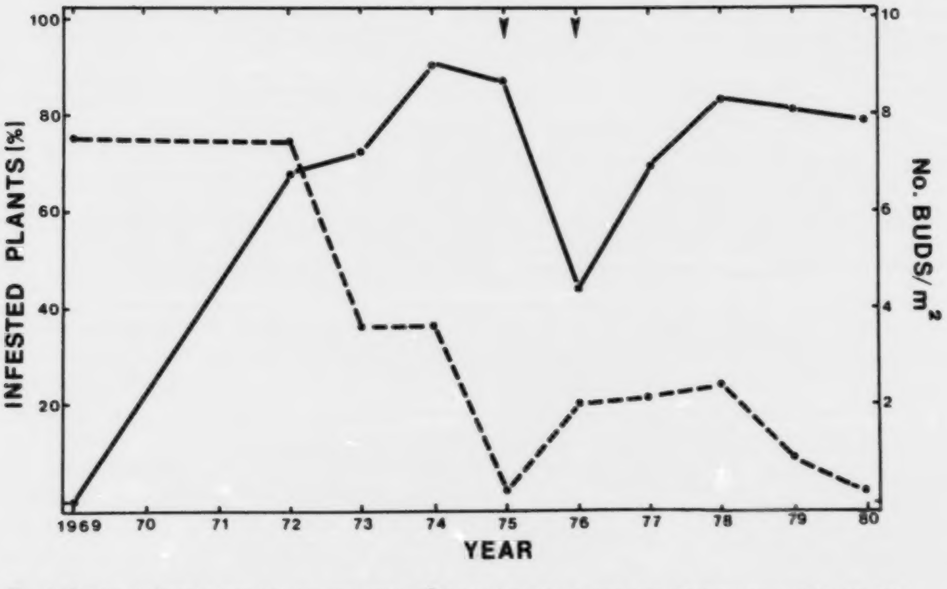

Fig. 2. Percent infested plants (*) and no. buds/m² (●) in Pulaski County site, Virginia, from 1969–80; field mowed during year (▼).

Because of the differences in plant vigor between resurgent thistles and pre-weevil-release thistles, density alone is not an accurate indicator of the population dynamics of the plants. More accurate would be the number of the buds/unit area, since plant reproduction is dependent on the number of thistle heads present. Even this is a conservative indicator of weevil influence, since buds on small plants are smaller than those on large plants. Thus, in spite of the resurgence in plant density, buds/m^2 is still significantly lower than the pre-release level for each site.

Other distinctive features of changes are the increase in egg density on the lateral heads as weevil population increases, and an increase in aborted heads (heads that fail to continue development because of the large number of weevil larvae feeding in them).

Table 2. Population dynamics of weevil–thistle in Pulaski County, southwest Virginia[1].

Observation	Year – Means[2]								
	1972	1973	1974	1975↓	1976↓	1977	1978	1979	1980
Plant infestation (%)	67.9 *bc*	72.5 *bc*	90.3 *d*	87.5 *d*	44.0 *a*	69.5 *bc*	83.4 *d*	81.0 *cd*	78.5 *bcd*
Terminal bud infestation (%)	47.6 *a*	72.4 *bc*	88.5 *d*	85.2 *d*	41.0 *a*	67.8 *b*	82.2 *cd*	80.4 *cd*	78.0 *bcd*
1st lateral bud infestation (%)	19.2 *a*	73.8 *c*	84.4 *d*	88.1 *d*	41.3 *b*	78.5 *cd*	83.8 *cd*	79.7 *cd*	77.8 *cd*
2nd lateral bud infestation (%)	18.8 *a*	77.9 *c*	83.8 *cd*	91.9 *d*	45.9 *b*	82.5 *cd*	84.4 *cd*	77.8 *c*	75.2 *c*
No. eggs/terminal bud	6.7 *bc*	6.7 *bc*	11.4 *d*	15.7 *e*	2.9 *a*	3.7 *ab*	7.1 *c*	8.8 *cd*	11.8 *d*
No. eggs/1st lateral bud	1.4 *a*	4.8 *bc*	9.3 *de*	12.7 *f*	2.0 *ab*	3.9 *ab*	6.9 *cd*	8.6 *de*	11.2 *ef*
No. eggs/2nd lateral bud	0.5 *a*	5.8 *cd*	8.7 *e*	11.8 *f*	2.3 *ab*	4.2 *bc*	6.8 *cde*	8.5 *de*	12.0 *f*
Aborted terminal bud (%)	0.3 *a*	3.0 *ab*	16.8 *d*	10.5 *c*	4.6 *b*	5.3 *b*	19.2 *d*	18.1 *d*	17.3 *d*
Aborted 1st lateral bud (%)	0 *a*	1.0 *ab*	5.2 *cd*	5.6 *cd*	0 *d*	3.0 *bc*	1.3 *ab*	6.4 *d*	11.6 *e*
Aborted 2nd lateral bud (%)	0 *a*	2.9 *bc*	2.2 *ab*	5.2 *cd*	0 *a*	3.7 *bc*	2.1 *ab*	4.9 *cd*	6.7 *d*
No. buds/plant	8.4 *d*	4.8 *c*	5.2 *c*	1.9 *a*	2.1 *a*	2.0 *a*	3.9 *bc*	3.0 *ab*	2.3 *ab*
Thistle density (no./m^2)	0.89*e*	0.76*d*	0.70*cd*	0.12*a*	0.97*ef*	1.03*f*	0.62*c*	0.31*b*	0.09*a*
Plant height (m)	1.4 *d*	0.9 *bc*	1.0 *c*	0.8 *bc*	0.7 *ab*	0.5 *a*	1.0 *c*	0.9 *bc*	0.8 *bc*
No. adult weevils encountered (total)	2	27	80	129	2	6	34	20	23
No. buds/m^2	7.5 *e*	3.6 *d*	3.6 *d*	0.2 *a*	2.0 *c*	2.1 *c*	2.4 *c*	0.9 *b*	0.2 *a*
Bud reduction (%)	0 *a*	52 *b*	52 *b*	97.3 *d*	73.7 *c*	72.0 *c*	68.0 *bc*	88.0 *d*	97.3 *d*

[1] 100 *R. conicus* released in June 1969; (observations based on 1000 plants); arrow indicates year when pasture was mowed.
[2] Means followed by the same letter for each row are not significantly different ($P < 0.01$, Duncan's MRT).

Disruption of the field by mowing or cultivation was accompanied by an increase in thistle density in the subsequent year. This shows the importance of grass competition in restricting thistle growth. The number of adult weevils encountered on the plants during the surveys also followed the general pattern of gradual increase and decrease of egg numbers. Thistle bud density over the years stabilized around 0.2–0.3 buds/m^2. This represents a reduction of 80% after the explosive phase at one of the sites, while reductions reach 97% in the other, where initial thistle density was much higher.

The impact of *R. conicus* on bud density is clearly illustrated in Figs. 1 and 2. In both instances, plant density is greatly affected by competition of grass. Thus overgrazing or misuse of land after establishment of the weevils tends to perpetuate the thistle problem. The decline in thistle numbers does not continue indefinitely even with successful establishment of biocontrol agents; population increases in plant density do occur after the explosive phase of weevil increase. The trend, however, continues towards a lower thistle population over time if weevil numbers increase again. These results confirm the potential of *R. conicus* in suppressing musk thistle on a long-term basis. The observations at these two sites clearly emphasize the need for proper land management, without which the full potential of *R. conicus* cannot be achieved.

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Period of Maximum Host Stress During Development of Galls of *Urophora cardui* (Diptera: Tephritidae) on Canada Thistle (*Cirsium arvense*)

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Abstract

Morphological evidence suggests that stress exerted by the gall of *Urophora cardui* on *Cirsium arvense* is greatest during the growth phase of gall development. During the *c.* 20 day growth phase, undifferentiated host tissue proliferates. Following this, the maturation phase begins, wherein cell proliferation ceases and tissues differentiate into distinct nutritive and lignified zones. Using insecticide to kill larvae inside growth phase galls causes tissues near the larval chambers to revert to wound callus, whereas outer tissues enter into the maturation phase. However, there is little alteration of gall tissue morphology if larvae are killed in maturation phase galls. This indicates that larvae continuously maintain tissues is an active state throughout the gall growth phase, but cease provoking gall growth at the end of this phase, thus initiating gall maturation. The resulting stable tissues in maturation phase galls probably do not require as much of the host's resources as do the proliferating tissues of the growth phase gall.

Période de Perturbation Maximale des Plantes Hôtes Pendant le Développement des Galles de *Urophora cardui* (Diptère: Tephritidae) sur le Chardon des Champs *Cirsium arvense*

D'après certains preuves morphologiques, les effets perturbateurs de la galle de *Urophora cardui* sur *Cirsium arvense* s'exercent au maximum pendant le pèriode de croissance de la galle. Pandant l'étape de croissance d'environ 20 jours, les tissus hôtes prolifèrent sans différenciation. Au bout de cette période, commence l'étape de la maturation, où la prolifération des cellules cesse et des zones distinctes de tissus nourriciers et lignifiés se forment. L'utilisation d'insecticides pour tuer les larves à l'intérieur des galles en période de croissance provoque la formation de callosités sur les tissus adjacents aux enveloppes larvaires, tandis que les autres tissue se rendent à maturation. Par contre, la modification de la morphologie des tissue des galles est négligeable lorsque les larves meurent dans les galles déjà à l'état de maturation. Ces observations indiquent que les larves maintiennent constamment les tissue vivants pendant la période de croissance des galles, mais cessent de favoriser la croissance de cells-ci à la fin de cette période, ce qui provoque la maturation des galles. Les tissus stables des galles à l'étape de maturation n'épuisent probablement pas autant les ressources des plantes hôtes que les tissus qui prolifèrent au cours de la croissance des galles.

Introduction

The gall-forming fly, *Urophora cardui* (L.) (Diptera: Tephritidae), was introduced into Canada in 1974 as part of an ongoing biocontrol program against Canada thistle, *Cirisum arvense* (L.) Scop. (Compositae) (Peschken *et al.* 1982). The narrow host range exhibited by gall-formers (Shorthouse and Harris 1985) and the successful use of a tephritid gall-former against a rangeland weed in Hawaii (Bess and Haramoto 1972), influenced the decision to use this, and other gall-formers as weed control agents in Canada. Initial laboratory studies demonstrated that the gall induced by *U. cardui* causes a reduction in the growth of Canada thistle for about 4 wks after oviposition (Peschken and Harris 1975). However, subsequent field evaluations made in successful release areas indicated that the gall does not sufficiently stress its host to cause significant reduction in growth over the season and that other biological control agents against Canada thistle are required (Peschken *et al.* 1982).

Any thistle control program that employs several biocontrol agents such as *U. cardui* should be coordinated to maximize the deleterious effect of the agent on the weed and to minimize effects of interference between different agents. Therefore it is necessary to identify the period of time when *U. cardui* larvae are stressing their host and when the gall-formers are likely to be affected by other biocontrol agents. The purpose of this paper is to use results obtained from studies of the developmental biology of the *U. cardui* gall system (Lalonde and Shorthouse 1984, 1985; Shorthouse and Lalonde, unpubl. data), to identify these critical periods in gall development.

Methods and Materials

Galled and ungalled plants were obtained from a growth chamber culture maintained at Laurentian University. Ungalled host tissue and material from galled tissues at all stages of development were prepared for histological examination. Larvae were dissected from galls at all developmental stages, oven-dried, weighed and instar was determined. In addition, systemic insecticide was applied to plants bearing galls at different developmental stages. Gall tissue from insecticide-treated plants was then prepared for histological examination and compared with untreated gall tissue.

Results and Discussion

The gall induced by *U. cardui* larvae passes through four developmental phases from egg hatch to adult emergence from senescent galls in the spring. These phases are: initiation; the growth phase; the maturation phase; and dehiscence.

Initiation occurs after second instar larvae hatch (7–10 days after oviposition) and tunnel down into immature stem tissues. Larval tunnelling induces the formation of wound callus in stem tissues posterior to the larvae. Once larvae cease tunnelling, cells of pith and procambium nearest to their chambers lose their normal polarity and begin to divide. As soon as host tissue begins to proliferate under the direction of the gall insect, the gall is considered to have entered the growth phase.

Gall growth becomes apparent 12–20 days after oviposition as a lateral expansion of the stem beneath a vegetative shoot. During the gall growth phase, a network of procambial tissue develops within the proliferating gall parenchyma. This tissue anastomoses with the vascular system of the ungalled portion of the host stem. The callus tissue formed by the initial tunnelling of second instar larvae expands as gall growth proceeds to form a well-defined zone above each larval chamber. In addition, patches of cells adjacent to the larval chambers become cytoplasmicly dense and accumulate starch grains and lipid-like droplets. These cells are consumed in small quantities by the larvae and are termed primary nutritive cells. Throughout the gall growth phase, larvae remain in the second instar and grow very little.

When insecticide was applied to galls during the growth phase, cell proliferation ceased earlier than in untreated controls. Callus tissue already present remained unchanged and primary nutritive tissue rapidly changed to callus, expanded into the larval chambers, and crushed the dead larvae. In the outer portion of the gall, gall parenchyma lignified and the procambial tissue matured into xylem and phloem (Fig. 1).

Approximately 20 days after the onset of the gall growth phase, cell proliferation ceases and the gall enters its maturation phase. During this phase, a thick zone of cytoplasmicly dense secondary nutritive cells develops from procambial initials in the tissue surrounding the larvae while outer gall tissues lignify. The region of callus above each larval chamber remains unchanged throughout this phase (Fig. 1). Shortly after the onset of gall maturation, larvae moult to third instar and begin feeding on secondary nutritive tissue. Larvae are fully grown within 24 days, or 60 days after oviposition.

When insecticide was applied to plants bearing maturation phase galls, larvae died, but most gall tissues remained unchanged (Fig. 1). However, this was not true for the secondary nutritive tissue. These cells did not lose their dense cytoplasm or revert to callus, but the internal cell structure gradually became increasingly amorphous, and bacteria often appeared within the cytoplasm.

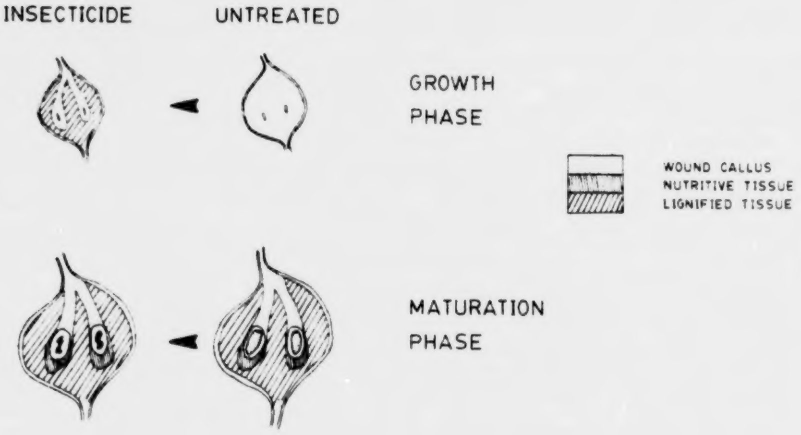

Fig. 1. Effect of application of systemic insecticide to growth phase and maturation phase galls of *Urophora cardui* (L.).

Dehiscence occurs in the spring when callus tissues in the gall degrade, opening channels through lignified tissue to the outside of the gall for emerging adults.

Of the four phases of gall development, the gall growth phase is probably the most critical, both in terms of the success of the gall-former and in terms of stress placed on the host plant. Once larval control is removed during this phase by insecticide treatment, gall tissues quickly become callus or lignify. This indicates that growth phase tissues are maintained in an active state by second instar larvae and that removal of larval influence allows the plant to convert gall tissue to inactive callus and halt further tissue proliferation. Also, the structural similarity between insecticide-treated growth phase galls and normal maturation phase galls suggests that normal gall maturation is triggered by a similar stimulus. Possibly the process of inducing formation of secondary nutritive tissue halts proliferation of gall parenchyma and initiates lignification.

Proliferation of host tissue during the growth phase draws on plant resources which could otherwise be committed to flower production or to augmentation of root reserves. Stored carbohydrates in roots of *C. arvense* are at their lowest level during the early phases of inflorescence development (Hodgson 1968), when early stage galls are likeliest to be present (Zwölfer *et al.* 1970). Consequently, it appears that galls of *U. cardui* develop on their host when it is most susceptible to stress.

There is apparently little or no tissue proliferation in the *U. cardui* gall following formation of secondary nutritive tissue. The minimal reaction observed when insecticide was applied to maturation phase galls also indicates that gall tissues are no longer maintained at a very high level of activity. Because minimal stress is exerted on the host once the maturation phase begins, thistles are probably able to begin making up reserves lost while the gall was growing. This may explain the aforementioned discrepancy between results obtained by Peschken and Harris (1975) and Peschken *et al.* (1982).

The 20 day period of the gall growth phase encompasses the time when *U. cardui* larvae may be sensitive to interference from other weed control agents. Gall tissue accumulated during this phase is converted to food for growing third instar larvae in the form of secondary nutritive tissue. If thistles are seriously stressed by other insects or pathogens while *U. cardui* galls are still growing, larvae may be unable to induce the growth of sufficient gall tissue. I believe that this would result in a reduced production of secondary nutritive tissue in the maturation phase, ultimately producing weaker, less fecund adults.

Galls accumulate all larval food in the form of secondary nutritive tissue at the onset of the maturation phase. Secondary nutritive tissue is stable, even in the absence of living larvae. Thus third instar larvae feeding in maturation phase galls are unlikely to be affected by interference from other thistle biocontrol agents. Larvae will only be seriously impaired during the gall maturation phase if their host is stressed to the point of death and nutritive tissues desiccate before they finish feeding.

The inclusion of *U. cardui* in a thistle control program thus may require selection of other biocontrol agents which attack the weed either prior to oviposition by adults or after galls have ceased to grow. Such a strategy would maintain a constant level of stress on thistles without adversely affecting *U. cardui* larvae. Further research should be undertaken to quantify the stress levels imposed by *U. cardui* galls on Canada thistle and to determine if interference from other biocontrol agents seriously affects the success of *U. cardui*.

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Effects of Duration of Low Temperature Exposure on Post-Diapause Development of Overwintering *Urophora affinis* and *U. quadrifasciata*

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Abstract

Duration of low temperature exposure has been shown to be an important factor regulating diapause development and duration and synchrony of post-diapause development in many insects. This can serve to synchronize insect emergence with availability of hosts and mates. Laboratory studies were undertaken to evaluate effects of low temperature exposures (4–6°C; 12 h photoperiod) ranging from 0 to 273 days on overwintering larvae and subsequent emergence of adult *Urophora affinis* and *U. quadrifasciata* subjected to 24°C and 16 h photoperiod. The rate of adult fly emergence was inversely related to duration of cold treatment. Emergence of adults of both species occurred without chilling, however the mean time to emergence for *U. affinis* was more than twice that of *U. quadrifasciata*. Prolonged low temperature exposure (> 200 days) resulted in similar emergence times for both species. Duration of low temperature exposure appears to be an important factor regulating post-diapause development and emergence of these insects.

Effets de la Durée d'Exposition à de Faibles Températures sur le Développement Postdiapause de *Urophora affinis* et *U. quadrifasciata* au Cours de l'Hibernation

D'après les études, la durée de l'exposition à de faibles températures constitue un important facteur qui influe sur le développement des diapauses et sur la durée et la synchronisation du stade postdiapause chez de nombreux insectes. Le paramètre peut servir à s'assurer que l'apparition des insectes coincide avec celle des hôtes et des mâles ou femelles pour la reproduction. Des études en laboratoire ont été effectuées pour évaluer les effets des expositions à faible température (4 à 6°C; photopériode de 12 heures) durant des périodes de 0 à 273 jours sur les larves hibernantes et l'apparition ultérieure des adultes de *U. affinis* et *U. quadrifasciata* soumis à une température de 24°C et à une photopériode de 16 heurs. La vitesse d'apparition des insectes adultes était inversement proportionnelle à la durée de l'exposition au froid. Les adultes des deux espèces apparaissaient sans exposition au froid, mais la durée moyenne du stade pré-émergence pour *U. affinis* étaient deux fois plus élevés que pour *U. quadrifasciata*. Au cours des essais d'exposition prolongée à de faibles températures (plus de 200 jours) les périodes d'émergence étaient similaires pour les deux espèces. La durée de l'exposition à de faibles températures semble constituer un important facteur influant sur le développement postdiapause et l'apparition de ces insectes.

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Reaction of Safflower Cultivars to *Puccinia jaceae*, a Potential Biocontrol Agent for Diffuse Knapweed

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Abstract

Puccinia jaceae was tested on four safflower cultivars, US-10, S208, Rehbein, and Hartman, under growth chamber conditions. It was capable of infecting all four cultivars with fully susceptible pustules on the cotyledons. On the first set of true leaves, resistant-type pustules often surrounded by chlorotic and necrotic areas occurred, and no infections were observed on upper leaves from any of these cultivars. *P. jaceae* can be cultured on cotyledons of safflower, cultivar S208, for at least four generations without noticeable change in virulence on safflower as well as on diffuse knapweed. The effect of *P. jaceae* on development of safflower appears to be minimal under growth chamber conditions. The threat that this rust could pose to the safflower production, if released for biocontrol of diffuse knapweed, is discussed.

Réaction des Cultivars de Carthame a *Puccinia jaceae*, un Agent Biologique Potentiel de Lutte Contre la Centaurée Diffuse

Puccinia jaceae a été mise à l'essai sur quatre cultivars de carthames, soit US-10, S208, Rehbein et Hartman, dans des conditions de chambre climatisée. Elle a infesté les quatre cultivars et a provoqué la formation de pustules entièrement susceptibles sur les cotylédons. La première série de feuilles authentiques présentait des pustules résistantes, entourées de zones chlorotiques et nécrotiques, et aucune infestation n'a été observée sur les feuilles supérieures des quatre cultivars. *P. jaceae* peut subsister sur les cotylédons du cultivar S208 pendant au moins quatre générations sans modification notable de sa virulence à l'égard du carthame ou de la centaurée diffuse. L'auteur traite des risques que cette rouille pourrait faire courir à la production de carthame si elle était utilisée comme agent biologique de lutte contre la centaurée diffuse.

Introduction

Diffuse knapweed (*Centaurea diffusa* Lam.; Compositae) is a herbaceous weed of European origin which is spreading rapidly on the dry grasslands of western Canada and the U.S.A. (Watson and Renney 1974; Harris and Cranston 1979). Biological control is considered to be the most satisfactory solution, and several insects have been released and established in Canada for this purpose. They have inflicted damage, but not enough to control diffuse knapweed, and additional biocontrol agents are needed to increase the pressure on diffuse knapweed (Harris and Myers 1984).

Several rust species have been reported from *Centaurea* spp. in Europe (Gaümann 1959; Gayot 1967; Ialongo and Boldt 1977) and in 1978 a rust, *Puccinia jaceae* Otth. (Uredinales) was collected from diffuse knapweed in Eastern Europe (Watson *et al.* 1981). This rust was found to be virulent on diffuse knapweed collected from 15 different locations in western Canada and northwestern United States, indicating that diffuse knapweed populations in North America generally are highly susceptible to this rust and that host plant resistance should not restrict its effectiveness as a biocontrol agent (Watson and Alkhoury 1981).

Tests under growth chamber conditions (Watson and Alkhoury 1981) revealed that *P. jaceae* was capable of infecting safflower (*Carthamus tinctorius* L.; Compositae) in the seedling stage, but later plant stages became resistant. Before release as a biocontrol agent on diffuse knapweed can be approved, it is essential to test its capability to develop on, and the effect, if any, it might have on safflower, a field crop cultivated relatively close to infested diffuse knapweed areas (Mortensen 1985).

The purpose of these experiments was to test susceptibility of safflower cultivars currently grown in Montana to *P. jaceae*, and the effect of the rust infections on safflower plants. The question of whether or not the rust can survive on safflower was tested by culturing it for successive generations of urediniospores on safflower cotyledons under growth chamber conditions.

Materials and Methods

European knapweed rust, *P. jaceae*, used in these studies was collected from diffuse knapweed in Rumania (Watson *et al.* 1981). Two isolates of this rust, R11 and R13h2, originating from single pustules on infected diffuse knapweed leaves that had been stored in liquid nitrogen for more than a year, were increased on diffuse knapweed in a growth chamber under quarantine conditions at Regina Research Station. Urediniospores used for inoculations were either freshly harvested from plants, or spores had been stored in glass vials in liquid nitrogen. Isolate designations refer to collection sites in Rumania (Watson *et al.* 1981).

Plants for the experiments were grown from seeds in plastic pots (15 cm diam.) in top soil (sandy-loam) mixed with sphagnum (3:1) under greenhouse conditions, temperature 18–24°C with a 16 h light period from 400 watt high pressure sodium lights. Seeds of safflower cultivars were obtained from safflower breeder, J.W. Bergman, Montana Agricultural Experiment Station, Sidney, Montana.

Plants were inoculated by atomization with a suspension of urediniospores in distilled water until runoff (concentration: approx. 0.5 million spores/ml). Inoculated plants were incubated in a dew-simulating chamber in total darkness for 18 h at 14±1°C. After the dew period the plants were allowed to dry slowly before being placed in a growth chamber at 24±2°C with a 16 h daily light period from cool flourescent and incandescent lights.

This study included three separate experiments:

Susceptibility test of safflower cultivars to P. jaceae. Five pots (five plants/pot) from each of four safflower cultivars, US-10, S208, Rehbein and Hartman, were inoculated separately with isolates R11 and R13h2 on 10–12 day-old seedlings, with cotyledons and the first set of true leaves developed. Infection type of pustules were recorded 14–16 days after inoculations. The experiment was repeated by inoculating three pots (2–3 plants/pot) from each cultivar with the two isolates at the 6–8 leaf stage (just prior to flowering). Infection type of pustules were recorded 17 days and again 45 days after inoculation. Control plants of inoculated diffuse knapweed plants were included with each test. The rating of infection type was done on a scale from 0 to 9:

0. Immune, no sign of infection;
1. Resistant, necrotic or chlorotic spots, no visible pustules;
2. Resistant, minute pustules (hardly visible) with very little sporulation, necrotic or chlorotic areas around pustules;

3. Moderately resistant, very small pustules (< 0.2 mm diam.) with little sporulation and chloratic areas around pustules;
4. Moderately resistant, small pustules (< 0.4 mm diam.) with some sporulation, chlorotic areas around pustules common;
5. Moderately susceptible, medium-sized pustules (< 0.6 mm diam.) with moderate sporulation, chlorotic areas around pustules occurs frequently;
6. Moderately susceptible, fair-sized pustules (< 0.8 mm diam.) with moderate to fair sporulation, slight chlorotic area around pustules can occur;
7. Susceptible, fair-sized pustules (< 1 mm diam.) with fair sporulation;
8. Susceptible, large pustules (< 1.3 mm diam.) with considerable sporulation; and
9. Highly susceptible, large pustules (> 1.3 mm diam.) with heavy sporulation.

Effectivity test of P. jaceae *on safflower.* Five pots of 19-day-old safflower (just prior to flowering) and five pots of 13-day-old plants (4–6 leaf stage when cotyledons were still in good condition) of cultivar S208 were inoculated with two isolates of *P. jaceae*, R11 and R13h2. Control plants for each age group and isolate were sprayed with distilled water. Control pots of diffuse knapweed were included with each test. Inoculated plants were rated for infection type 18 days after inoculation, reinoculated and rated again 16 days after the last inoculation. All plants were harvested 42 days after the first inoculation by cutting stems at the soil level and washing roots free of soil. Stems (including leaves and flower heads) and roots from each pot were dried for 24 h at 80°C and weighed separately. At harvest most plants from the young plant stage had completed flowering. Results were calculated as relative yield of dry matter in percent of controls.

Survival test of P. jaceae *on safflower.* Seedlings of safflower, cultivar S208, were inoculated with the two isolates, R11 and R13h2 (5 pots of 5 plants/isolate). Two wks after inoculation, infection type and density of pustules were recorded, then the urediniospores were harvested, suspended in water and inoculated on a new set of safflower seedlings and the plants from which the spores were harvested. This procedure was repeated four times, thus culturing the two isolates for four generations of urediniospores on safflower seedings.

Results

All four safflower cultivars tested were susceptible to the two isolates, R11 and R13h2, of *P. jaceae* on the cotyledons, but the first set of true leaves showed resistant reaction as indicated with infection types 7 or higher and 1–4, respectively (Table 1). The infection level on the cotyledons was high, with 50% or more of the leaf area covered with pustules, whereas, normally, only a few (1–5) developed on the first set of true leaves and very seldom were pustules observed on the second set of true leaves. Upper leaves were totally resistant to *P. jaceae*. Infected leaves senesced faster than uninfected leaves. As indicated in Table 2 it was possible to measure a slight reduction in yield of dry matter on infected safflower plants compared to uninfected plants. Safflower plants 19 days old at inoculation were least affected with little reduction in dry matter. Younger safflower plants (13 days old at inoculation) were affected more, especially the roots, where a 20% reduction in dry matter was observed for infected plants compared to uninfected safflower plants. No detectable difference was observed between the two isolates of *P. jaceae*, therefore, the results from both isolates were combined in Table 2.

The experiment to test the survival of *P. jaceae* through successive generations of urediniospores on safflower seedlings showed that both isolates could be successfully cultured on cotyledons of safflower for at least four generations without apparent loss in virulence on diffuse knapweed nor was increase in virulence on safflower detected.

Discussion

The data obtained in above experiments are in good agreement with data obtained by Watson and Alkhoury (1981), who tested two isolates of *P. jaceae* on six other cultivars of safflower. Based on these independent studies it can be concluded that safflower generally is susceptible to *P. jaceae* in the seedling stage, and that older safflower plants are resistant. Present studies show that safflower in the seedling stage is a satisfactory host for this rust to develop and reproduce on under growth chamber conditions, and also that safflower is slightly stressed when infected with *P. jaceae* in the early seedling stage.

Table 1. Infection types recorded on safflower cultivars and diffuse knapweed inoculated with *Puccinia jaceae* Otth. under growth chamber conditions.

Host plant	*P. jaceae* isolate	Infection type (scale: 0–9)[1]	
		Cotyledons	First set of true leaves
Carthamus tinctorius L.			
US-10	R11	8	2–3
	R13h2	7	2–4
S208	R11	7	1–3
	R13h2	7	1–4
Hartman	R11	7	1–4
	R13h2	7	1–3
Rehbein	R11	7	1–4
	R13h2	7	2–4
Centaurea diffusa Lam.	R11		9
	R13h2		8

[1] 0 = immune; 9 = fully susceptible pustules.

It would be safe to assume that if infection can occur under growth chamber conditions, it can also occur under natural conditions. The next question is then, how likely will *P. jaceae* be exposed to safflower in the susceptible stage under natural conditions if released on diffuse knapweed in North America? Safflower is grown commercially on a considerable hectarage in central and eastern Montana and the Dakotas (Bergman *et al.* 1979). This is relatively close to diffuse knapweed infested areas in western Montana, Idaho and British Columbia. Thus it could be possible to have air-borne urediniospores from infected diffuse knapweed plants reach safflower crops. However, considering that safflower is only susceptible in the seedling stage, it is unlikely that the rust would be far enough advanced on diffuse knapweed in spring to produce a sufficient number of urediniospores that would allow spread to safflower crops while still susceptible. Should urediniospores happen to reach safflower seedlings, infections could occur, but chances that successive generations of urediniospores will develop on safflower within the susceptible stage is minimum. Thus, the rust has little chance of surviving on safflower. Since *P. jaceae*, according to Watson and Alkhoury

(1981) and unpublished studies conducted at the Regina Research Station, has potential for biocontrol of diffuse knapweed in North America, and since there is a need for additional biocontrol agents to suppress diffuse knapweed sufficiently in rangeland (Harris and Myers 1984), I feel that the slight chance that *P. jaceae* could pose a threat to safflower production might be worth taking in comparison to the added pressure this rust could inflict on diffuse knapweed.

Experiments will be conducted in France in 1985 to test *P. jaceae* on safflower cultivars under field conditions. If it does not survive on safflower through the season in these field tests, I feel that it will be safe to release *P. jaceae* on diffuse knapweed in North America.

Table 2. Yield in dry matter of safflower plants, cultivar S208, inoculated with *Puccinia jaceae* Otth. relative to non-inoculated plants.

Plant material	Age of plants at inoculation (days)	Relative yield (dry matter)[1] Control	Inoculated
Leaves and stems:	19	100	97.1
	13	100	92.5
Roots:	19	100	95.9
	13	100	79.7

[1] Plants were harvested 42 days after first inoculation (all plants had completed flowering). Results are based on data from two isolates of *P. jaceae* (average of 10 replications).

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Density and Survival of *Urophora stylata* (Diptera: Tephritidae) on *Cirsium vulgare* (Compositae) in Relation to Flower Head and Gall Size

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Abstract

Infestation of flower heads of *Cirsium vulgare* by *Urophora stylata*, and the subsequent mortality of *U. stylata* and its causes were studied at sites in Britain and West Germany. No clear relationships were found for infestation and mortality with the density or size of plants. The size of head, and the timing of its development are, however, important. Infestation is greater in large (and early maturing) heads than in small (and late developing) ones. Ectoparasites cause greatest mortality in galls in small heads; the endoparasite *Eurytoma tibialis* is indiscriminate, while deaths caused by Lepidoptera are greatest in large galls in large heads, although small heads with galls suffer more damage than those without. Overall survival of *U. stylata* is best in small galls in large heads and thus relates positively to levels of infestation. The relationship is not, however, perfect, and the reasons for this are discussed.

Densité et Taux de Survie de *Urophora stylata* sur *Cirsium vulgare* en Fonction de la Taille des Capitules et des Galles

l'infestation des capitules de *Cirsium vulgare* par *Urophora stylata*, et la mort subséquente de *U. stylata* et ses causes ont été étudiées en des emplacements de Grande-Bretagne et d'Allemagne de l'Ouest. Il n'existe aucun lien précis entre l'infestation ou le taux de mortalité et la densité ou la taille des plantes. Toutefois, la taille de la capitule et le moment de son développement constituent des facteurs importants. L'infestation est plus marquée dans les grands capitules (et à maturation précoce) que dans les petits capitules (et à maturation tardive). Les ectoparasites infestent principalement les plantes à petits capitules et entraînent leur mort, mais l'endoparasitoïde *Eurytoma tibialis* n'est pas sélectif en ce qui concerne la taille des capitules. Les grands capitules, atteints ou non de galles, et les petits capitules atteints de galles sont une source d'alimentation pour les chenilles qui constituent une important cause de mortalité sur certains sites. Les petites galles des grands capitules offrent les meilleurs possibilités de survie à *U. stylata* mais, en présence de fortes densités, ces conditions optimales sont rares; le rapport traite des raisons de ce phénomène.

Introduction

The gall fly *Urophora stylata* L. (Diptera: Tephritidae) infests flower heads of the Spear or Bull Thistle, *Cirsium vulgare* (Savi) Ten. (Compositae), in which its larvae induce hard, multilocular galls which reduce the production of viable seed by the plant (Redfern 1968, 1983; Zwölfer 1972).

Within the natural range of *C. vulgare*, the presence of this fly, and of other herbivores, may act to control the abundance of the plant (Zwölfer 1965; Redfern 1983). In North America where *C. vulgare* and other Cynareae (Compositae) introduced from Europe are serious agricultural weeds, *U. stylata* has been introduced as a biological control agent and achieves very high levels of infestation compared with most European populations (Harris 1984).

The life cycle and principal causes of mortality in *U. stylata* are well known (Persson 1963; Redfern 1968, 1983; Zwölfer 1972) and most causes can be determined after the event by inspection of gall-cells and their contents. Additional details of mortality and the biology of the parasitoids concerned are given in Claridge (1961), Varley (1937*b*, 1947) and Cameron and Redfern (1974).

Investigations of host-plant/gall fly interactions in *C. vulgare* and other Cynareae: Carduinae have concentrated on the effect on the plant (Zwölfer 1972; Baloch and Khan 1973; Harris 1980*a*, *b*; Myers and Harris 1980), on the regulation of the fly population (Varley 1947) and on aspects of the developing flower head which influence oviposition (Zwölfer 1972; Berube 1980). In this study, we concentrate on the effects of flower head size on probability of infestation, degree of infestation and subsequent mortality of *U. stylata* in populations within its natural range, and examine evidence that the pattern of infestation relates not only to food supply but also to the risk of death. The implications for the effectiveness of *U. stylata* as an agent of biological control of *C. vulgare* in areas where some mortality factors are absent is also briefly discussed, and related to more general hypotheses on foraging strategy (Hassell and Anderson 1984).

Table 1. Location of *Cirsium vulgare* (Savi) Ten. sites and dates of sampling.

Site	Grid reference	Altitude (m)	Habitat	No. plants in sample	Date of collection
Bayreuth University Campus, W. Germany (B82)	4470555326	350	Waste ground	5	10.viii.82
Rupertskapelle, W. Germany (R82, R83)	4456855310	390	Roadside verge	7 5	27.viii.82 14.viii.83
Oberwaiz, W. Germany (O82)	4462055340	430	Abandoned meadow	10	27.viii.82
Waldringfield, England (W82, W83)	150/TM 286443	< 15	Abandoned marshy meadow	8 5	20.xi.82 22.x.83

Materials and Methods

Spear thistle heads were sampled at four sites, three near Bayreuth, West Germany, and one at Waldringfield, Suffolk, England. All sites were sampled in 1982 and two resampled in 1983. Table 1 shows details of the sites.

At Bayreuth (B82) and Waldringfield (W82 and W83), the density of thistles was estimated using a point-centred method (Cottam and Curtis 1956), using random points within a gridded study area and measuring the distances from the points to the nearest thistle. The nature of the other sites made this technique impossible. At Oberwaiz (O82) and Rupertskapelle in 1982 (R82), an area was marked out and all thistles within it counted. No density estimate was carried out at Rupertskapelle in 1983 (R83).

At all sites except R82 and O82, an estimate of the degree of crowding, or proximate density, affecting each sample plant was obtained by counting the number of plants within a 5 m radius of the sample plant.

All heads of each sample plant were collected and bagged for subsequent laboratory examination. If numbers of heads were low, heads from the nearest neighbour were also collected, separately. In the laboratory, the size (maximum diam. between outer bracts) and state of development (bud, flower, dead) were recorded for each head, and their contained insect fauna was determined by dissection. For heads galled by *U. stylata*, the size of gall (maximum diam.), number of gall-cells and the fate of the contents of each were recorded. At some sites, drawings were made of each gall showing the position and fate of each cell. Other inhabitants of each head and any evidence of insect damage were also recorded. Methods of identifying causes of death are given in Redfern (1968).

Examination of the heads was a lengthy process and it was therefore necessary to deep-freeze some samples to preserve them prior to examination. This occasionally resulted in discolouration of *U. stylata* larvae, but comparisons with fresh-dissected material enabled such larvae to be assigned to appropriate categories without difficulty.

Although infestation by *U. stylata* varied between plants within each sample site, this variation was slight compared to between site variation and was, in any case, principally due to variation in infestation with head size, which is analysed in detail. For most purposes, therefore, all data from one site and year are pooled.

Results

Infestation by U. stylata *in Relation to Density, Size and Head Size of the Host Plant*

Table 2 gives the estimates of density, heads/plant, size of heads, % of heads infested and numbers of cells/head and cells/infested head. The point centre estimates were undoubtedly biased by the aggregated dispersion of the thistles and indicate only that density at Bayreuth (and, subjectively, at the other German sites) is considerably greater than at Waldringfield.

Estimates of proximate density, heads/plant and % of heads galled showed considerable variation between sites, but did not appear to be related.

The mean number of cells/head also varied markedly between sites. In all cases, the index of dispersion (variance/mean) was significantly > 1, indicating that cells were highly clumped in heads. There was no evidence of any relationship between degree of clumping and mean number of cells/head. Mean cells/head and mean head size were correlated ($r_4 = 0.87$, $p < 0.05$), as were mean cells/gall and the ratio variance:mean for head size ($r_4 = 0.86$, $p < 0.05$). Infestation was greater in populations of thistles with larger heads and, in populations of thistles with a high mean number of cells/infested head, the variation in head size was large relative to the mean. Mean head sizes were lower in 1983 than 1982 in the two sites sampled in both years, though in R 83 it is possible that further growth might have altered the mean.

Infestation by U. stylata *in Relation to Developmental Stage and Size of Head*

Details of % of heads with galls and number of cells/gall in relation to size and developmental stage of head are given in Appendix 1. No differences in either size or % of heads with galls could be detected between dead heads and those in full flower and so they are combined for comparison with buds.

Heads in bud were generally smaller than those that have completed their development. They were also heads whose development was late. Table 3 shows the range of bud size; the proportion of buds in each size class declined as the season advanced, except that heads of diam. 7 mm or less were always buds and (with only one exception) were never galled. Given the large size of some buds in the earliest

Table 2. Estimates of density, heads/plant and mean head size (± S.E.) of *Cirsium vulgare* (Savi) Ten. at the study sites, together with the levels of infestation and cells/gall of *Urophora stylata* L. Point centre estimates were not made in O82, R82 and R83 nor were proximate density estimates made at R82 and O82. In O82, an estimate of proximate density can be derived from the number of plants in an 85 m^2 plot. Plants were selected non-randomly at R83.

Site	Point centre plants/ha	Proximate density/m	Mean heads per plant	Head size			Overall % heads with galls	No. cells/head			Mean no. cells/gall
				Mean diam. (mm) $\bar{x}$	Variance S^2	$S^2/\bar{x}$		Mean $\bar{x}$	Variance S^2	Index of dispersion $S^2/\bar{x}$	
B82	350	0.16 ±0.04	64.2 ±44.4	14.30 ±0.23	21.50	1.50	10.7	0.38	1.95	5.13	3.59
R83	—	0.06 ±0.02	260.6 ±59.7	13.35 ±0.12	13.78	1.03	32.3	0.90	3.38	3.77	2.78
R82	—	—	50.1 ±17.6	19.04 ±0.36	42.75	2.24	62.9	2.53	9.45	3.73	4.02
O82	—	0.16	13.4 ± 3.1	22.33 ±0.68	60.24	2.70	87.6	8.22	63.40	7.71	9.38
W82	20	0.07 ±0.02	76.5 ±23.2	17.17 ±0.17	18.20	1.06	13.7	0.39	1.51	3.82	2.88
W83	10	0.01 ±0.004	76.8 ±35.4	14.07 ±0.22	17.75	1.26	8.3	0.28	1.25	4.43	3.40

Correlation coefficients: Head size $S^2/\bar{x}$ against mean cells/gall $r = 0.86$, $p < 0.05$. Mean no. cells/head against mean head size $r = 0.87$, $p < 0.05$.

sample B82, it is clear that late developing heads are smaller and, in the case of those still in bud in October and November (W82 and 83), probably never reach maturity. Heads < 8 mm in diam. are therefore omitted from further analysis.

Since % of heads with galls increased with head size (see below), the effect of developmental stage was examined within size classes. There are 18 possible comparisons (sample/size class categories in which both buds and fully developed heads occur), but in many of them, one or other category was represented by very small numbers. In 14 cases, the fully developed heads had a higher % of infestation and in 4, the buds did so ($X_1^2 = 5.5$, $p < 0.05$). Only two comparisons were individually significant (Table 4), both in the direction of higher infestation in developed heads. The number of cells/gall did not differ between buds and developed heads of the same size.

Table 3. Percent of heads which are buds by site and head size class. Sites arranged by date of sampling (— = no sample).

Sample	Date	Size classes (mm)						
		<8	8–11	12–15	16–19	20–23	24–27	28+
B82	10 Aug	100	92.8	73.3	31.0	3.5	6.7	—
R83	14 Aug	100	99.1	71.3	10.4	0	0	—
R82	27 Aug	100	98.6	60.7	0	0	0	0
O82	27 Aug	100	86.7	37.5	0	0	0	0
W83	22 Oct	100	61.4	17.5	3.1	0	0	—
W82	20 Nov	100	60.8	4.1	0.4	0	0	—

Table 4. Comparison of proportion of galled heads in buds and developed heads in two size classes of head at R83 (see text).

Head size:	12–15 mm			16–19 mm		
	Galled	Not galled	Total	Galled	Not galled	Total
Buds	61	231	292	2	17	19
Developed heads	71	46	117	116	47	163
Total	132	277	409	118	64	182
X^2		60.5			27.4	
p		<0.001			<0.001	

In all sites (and in both years), % of heads with galls and the mean number of cells/gall increased with increasing head size (Appendix 1 and Fig. 1). The increase in % infestation was most marked in samples with low overall % of galled heads and least at Oberwaiz, where the mean head size and overall % infestation were very high. There was, however, no relationship overall between % infestation and mean head size between sites.

Between sites, there was no relationship between % infestation and mean number of cells/gall in small heads, but signs of a positive relationship developed as head size increased (Table 5). This suggests multiple laying at high densities, when nearly all heads are galled.

This marked preference for large heads might simply be a function of space available for infestation. The achenes are arranged in a single plane and so the area of receptacle base should relate linearly to space available. This was not measured directly but can be estimated from head diameter. Since numbers of heads in some size-classes are small, any trends have been examined by amalgamating size-classes, and comparing the number of cells found in small (8–19 mm) and large (20+ mm) heads with the numbers expected if cells were distributed in proportion to area available (Table 6). In each case, there is an excess of cells in the large heads; i.e. the preference for large heads cannot be accounted for by available area alone. X^2 values for each comparison were all formally significant but it is doubtful if cells can be considered as truly independent (see below). Infestation of buds was erratic and not strictly comparable between sites. There was a negative relationship between the overall density of cells/unit area and the ratio of densities in large:small developed heads ($r = -0.87$, df 4, $p < 0.05$). At high levels of infestation, discrimination between heads declines.

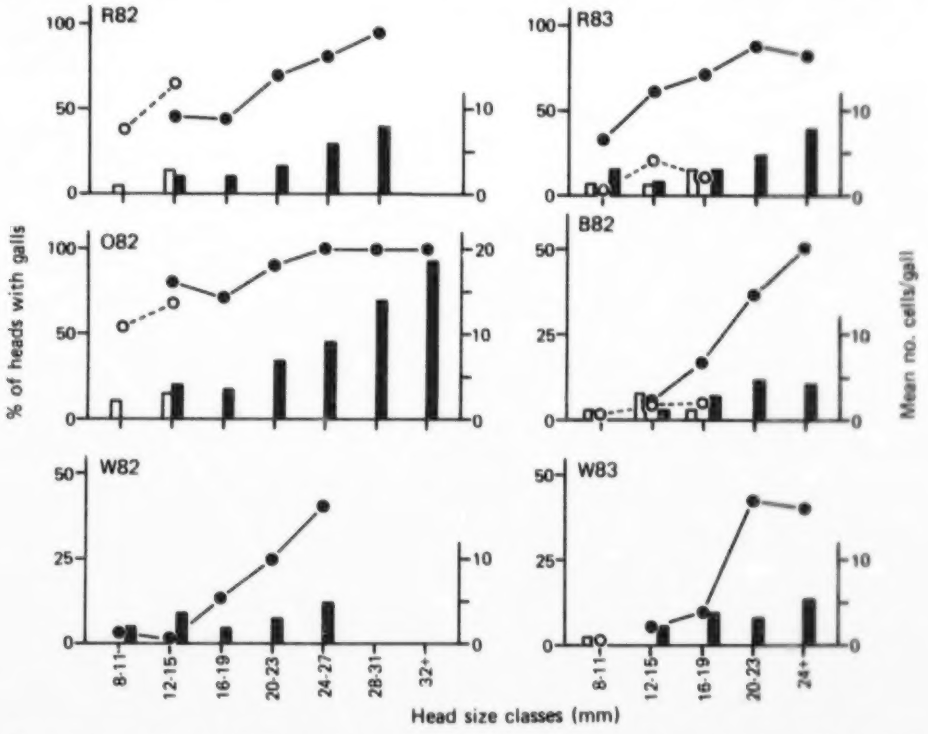

Fig. 1. Percent of heads with *Urophora stylata* L. and mean number of cells/gall by size of head in buds (○, □) and developed heads (●, ■) at six sites. R82, R83 = Rupertskapelle 1982 and 1983; O82 = Oberwaiz 1982; B82 = Bayreuth 1982; W82, W83 = Waldringfield 1982 and 1983.

Development of U. stylata *Relative to Head Size and Maturity*

At Oberwaiz and Waldringfield (both years) nearly all surviving *U. stylata* larvae were third instar and fully fed. In R82, sampled at the same time as Oberwaiz, 11 third instar larvae out of 657 (1.7%) were not fully fed. Of these, seven were found in buds of 8–11 mm diam. (64% of all survivors in this size class). In the two earlier samples (B82 and R83), there were more larvae not fully fed (Table 7). In both, the proportion not fully fed declined with increasing head size. Samples were not large enough to investigate any differences between buds and developed heads of the same size, and it is an open question whether larvae in small heads develop more slowly or start their development later, or both.

Table 5. Correlations between % of heads with galls and mean number of cells/gall between sites by head size and development. In buds, there is no entry for W83 when there were no galls in buds.

Head stage	Size class	r	p
Buds	8–11	0.43	ns
Developed	12–15	0.31	ns
Developed	16–19	0.27	ns
Developed	20–23	0.70	ns
Developed	24–27	0.88	<0.05

Table 6. Distribution of cells by stage of head, head size and relative areas available to be galled. Since proportion of buds varies with season, mean cells/unit area, number of cells expected (on assumption of equal nos./unit area), X^2 and ratio cells/unit area in large and small heads are all based on developed heads only. B = buds, D = developed heads.

Site	Head size (mm)	Relative area	Cells/area	No. cells		X^2 p	Ratio cells/area in heads $\frac{\text{D 20+}}{\text{D 8–19}}$
				Observed	Expected		
O82	B 8–19	25.1	1.07	27	—		
	D 8–19	69.7	1.02	71	94	6.2	
	D 20+	700.0	1.37	962	939	<0.05	1.34
	Mean		1.34				
R82	B 8–19	105.3	0.62	65	—		
	D 8–19	169.0	0.29	49	94	25.2	
	D 20+	1229.4	0.59	729	634	<0.001	2.03
	Mean		0.56				
R83	B 8–19	975.2	0.11	103	—		
	D 8–19	798.3	0.59	475	535	21.7	
	D 20+	360.8	0.83	300	240	<0.001	1.41
	Mean		0.67				
B82	B 8–19	397.5	0.04	15	—		
	D 8–19	246.8	0.09	23	56	32.0	
	D 20+	382.3	0.31	120	87	<0.001	3.44
	Mean		0.23				
W82	B 8–19	60.5	0.00	0	—		
	D 8–19	1075.9	0.06	62	126	65.8	
	D 20+	1085.3	0.18	191	127	<0.001	3.00
	Mean		0.12				
W83	B 8–19	120.6	0.002	1	—		
	D 8–19	551.2	0.08	45	74	42.5	
	D 20+	205.0	0.27	56	27	<0.001	3.37
	Mean		0.13				

Mortality in U. stylata

(a) General. The incidence of mortality and its causes at each site are given in Appendix 2 and summarized in Table 8. There was substantial variation between sites both in overall mortality and in that due to particular causes. Where sites were sampled in successive years, both overall mortality and that due to Lepidoptera and miscellaneous causes was higher in 1983.

Table 7. Numbers and proportions of *Urophora stylata* (L.) third instar larvae which are not fully fed in B82 and R83. (No dead not fully fed larvae were found in B82.)

	Bayreuth 1982			Rupertskapelle 1983					
Head size (mm)	Total surviving larvae	Larvae not fully fed No.	%	Total surviving larvae	Larvae not fully fed No.	%	Total dead larvae	Larvae not fully fed, dead No.	%
8 –11	2	2	100.0	4	3	75.0	8	5	62.5
12 –15	12	9	75.0	95	64	67.4	49	33	67.3
16 –19	15	7	46.7	141	40	28.4	78	36	46.2
20+	96	14	14.6	119	2	1.7	19	1	5.3

Overall mortality did not relate to cells/head or to cells/unit area, nor to time of sampling. Trends in overall mortality were followed by lepidopteran-caused deaths and those caused by unknown agencies, which were themselves weakly correlated (Table 8). Parasitism did not follow the same pattern; it correlated inversely with cells/unit area of head and this correlation was stronger in the ectoparasites than in the endoparasitic *Eurytoma tibialis* (Hymenoptera: Chalidoidea: Eurytomidae). Sparse infestations of *U. stylata* suffered more from parasitism than dense ones.

Further analysis of mortality is complicated. Cells in the same head were not independent in terms of mortality (there was an excess of all surviving and all dying in many cases), but the gall, or head, as a unit of sample was unsatisfactory because of the wide range of cells/head found. Standard statistical tests are thus technically invalid, even though the numbers of cells involved in particular comparisons were often large. Statistical tests were therefore generally avoided, the consistency of trends between samples being taken as the best guide to their reliability.

Table 8. (a) % mortality of *Urophora stylata* L. overall and by causes in relation to site and density/unit area of head. (b) Correlations between mortalities and density, and between selected mortality factors (all with 4 d.f.).

Site	Density cells/area	% mortality caused by						No. cells
		Overall	All parasites	Ectoparasites	*E. tibialis*	Lepidoptera	Other	
(a)								
O82	1.33	50.4	5.5	5.0	0.5	29.3	13.9	1060
R82	0.56	22.0	8.6	4.7	3.9	6.1	6.9	842
R83	0.41	59.1	12.9	3.0	9.9	25.7	19.3	878
B82	0.15	20.9	15.8	12.2	3.6	2.5	2.5	158
W82	0.11	20.9	17.8	17.8	0.0	1.6	1.6	253
W83	0.12	59.8	16.7	9.8	6.9	17.6	24.5	102

(b)

	Density	
	r	P
Overall	+ 0.26	ns
All parasites	− 0.94	< 0.01
Ectoparasites	− 0.60	ns
E. tibialis	− 0.32	ns
Lepidoptera	+ 0.65	ns
Other	+ 0.14	ns
Lepidoptera/other	+ 0.77	ns
Ectoparasites/*E. tibialis*	− 0.52	ns

(b) Mortality and head size. Figure 2 shows variation in mortality with flower head size. The two early samples (B82 and R83) showed no consistent trends but in the other four, mortality declined with increasing head size. *U. stylata* is safer in large heads and this is where it was found most frequently, both absolutely and in terms of cells/head area (see above).

Examination of individual causes of mortality required amalgamation of head size categories (Table 9). Excluding the two early sites where mortality may not be complete, ectoparasitism and miscellaneous deaths (mostly empty cells and shrivelled larvae) followed the trend seen in overall mortality, being lower in large heads. Deaths caused by *E. tibialis* showed no trend, however, and those caused by caterpillars actually increased in large heads in four of the samples. Causes of mortality are considered in more detail below.

(c) Mortality and cells/gall. Table 10 shows the variation in mortality with number of cells/gall. Some sites showed marked variation and others did not. Inspection of the original data indicated that for any given number of cells in a gall, mortality was lower in galls of larger size (measured diameter) and in larger heads. Gall diameter was, however, so closely connected to the other variables that it was not further analysed.

(d) Cells/gall, head size and mortality interactions. Cells/gall and head size were correlated and their covariation interacted with mortality. To retain large numbers of cells in each category, rather broad combinations of gall size and head size were used in analysis. To avoid excessive bias due to the lack of independence of cells in the same gall, only categories containing at least 20 cells in at least 5 galls were considered (Appendix 3).

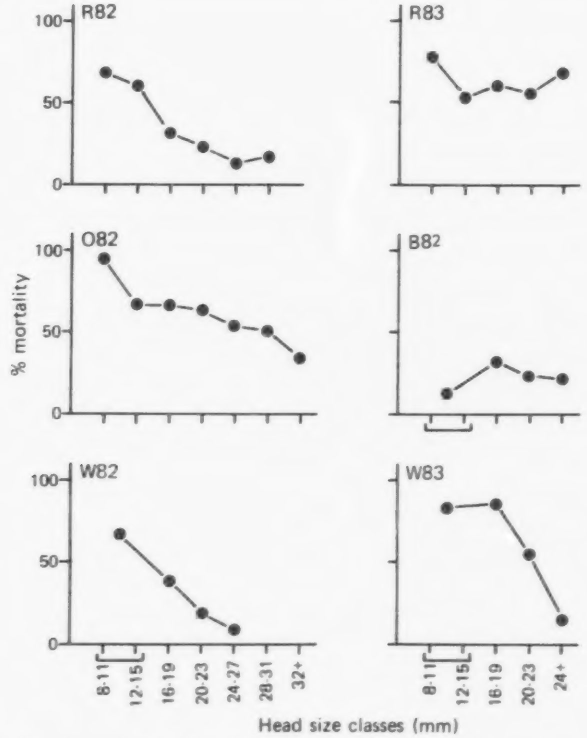

Fig. 2. Percent mortality of *Urophora stylata* L. by size of head. Sites as in Fig. 1.

Table 11 shows the variation in overall mortality at each site. With the exception of R83, within any cells/gall class, mortality declined with increasing head size but within any head size class, it increased with increasing number of cells/gall. In W83, where there were very few heads with more than six cells, a division on ±3 cells showed the same trend.

Cells in buds showed higher mortalities in O82 and R82 than those in developed heads in the same size range. The buds did, however, have lower median sizes within the range than the developed heads, and the relative importance of size and development could not be assessed.

Table 9. Incidence of mortality (%), both overall and by course in small and large heads by site. The mean given in the last row is not weighted for sample size.

Head size:	8–19 mm						20+ mm					
	% mortality caused by						% mortality caused by					
Site	Overall	Ectoparasites	*E. tibialis*	Lepidoptera	Other	No. cells	Overall	Ectoparasites	*E. tibialis*	Lepidoptera	Other	No. cells
O82	71.4	26.5	3.1	17.3	24.5	98	48.2	2.8	0.2	30.6	14.6	962
R82	53.5	19.3	4.4	1.8	28.0	114	17.1	2.3	3.9	6.7	4.2	729
R83	58.5	2.6	7.4	21.8	26.7	578	60.3	3.7	14.6	33.3	8.7	300
B82	23.7	13.2	10.5	0.0	0.0	38	20.0	12.2	1.1	3.3	3.4	120
W82	41.9	37.1	0.0	1.6	3.2	62	14.1	11.5	0.0	1.6	1.0	191
W83	84.8	15.2	8.7	30.4	28.3	46	39.3	5.3	5.3	7.1	21.8	56
Mean	55.6	19.0	5.7	12.5	18.4	156	33.2	6.3	4.2	13.8	9.0	393

Numbers were reduced when specific causes of mortality were considered, and trends were more erratic (Table 12). Ectoparasites showed a consistent trend in the four later samples, with mortality being highest in small heads. In the early samples, the incidence of ectoparasitism may not have been complete at the time of sampling. Cells/gall had little effect. The endoparasite, *E. tibialis*, showed no clear trends and, in the two samples from Rupertskapelle where it was reasonably common, it appeared to be evenly distributed with respect both to head size and cells/gall. It was, however, rare in buds.

Table 10. Overall mortality (%) of *Urophora stylata* L. larvae in galls containing differing numbers of cells. Categories of cells/gall increase in range with increasing number to balance numbers in each category (— = no sample).

Sites	Number of cells/gall				
	1–2	3–5	6–9	10–14	15+
B82	16.1	8.9	22.9	47.6	—
R82	38.5	21.6	19.3	17.7	—
R83	58.1	58.9	57.2	70.0	—
O82	62.2	50.6	36.5	48.6	55.1
W82	34.2	15.0	18.6	—	—
W83	46.7	65.1	54.2	—	—

Table 11. Variation in overall mortality (%) with head size and number of cells/gall (— = no sample, B = buds, D = developed heads.)

Site	Cells/gall	Head size (mm)			
		B8–19	D8–19	D20–27	D28+
B82	1–6	—	30.4	11.4	—
	7–12	—	—	32.0	—
R82	1–6	67.7	34.7	14.4	4.2
	7–12	—	—	20.7	15.9
R83	1–6	46.6	60.5	59.6	—
	7–12	—	65.2	59.3	—
O82	1–6	100.0	67.5	31.8	16.7
	7–12	—	—	44.7	16.5
	13+	—	—	80.9	50.2
W82	1–6	—	41.9	14.6	—
	7–12	—	—	12.5	—
W83	1–3	—	72.2	20.0	—
	4+	—	92.9	46.3	—

Larger heads (and larger galls) might afford some protection from parasitism; if this is so, it appears to work only for the ectoparasites. In the three sites for which information is available and in which numbers of parasites are adequate, the ectoparasites tended to attack *U. stylata* larvae near the edge of the gall by comparison with *E. tibialis* (Table 13). Since number of cells/gall had little effect on ectoparasitism, it may be that in large heads the difficulty of detecting a small gall balances the difficulty of penetrating a large one.

Deaths caused by Lepidoptera showed one consistent trend: an increase as number of cells/gall increased, though there was a weak trend (reversed in W83) for small

Table 12. Incidence of particular causes of mortality (%) by site, head size and number of cells/gall (— = no sample).

Site	Head size (mm)															
Cells/gall	Buds	Developed heads			Buds	Developed heads			Buds	Developed heads			Buds	Developed heads		
	8–19	8–19	20–28	28+	8–19	8–19	20–28	28+	8–19	8–19	20–27	28+	8–19	8–19	20–27	28+
B82																
1–6	—	13.0	7.1	—	—	17.4	1.4	—	—	0.0	2.9	—	—	0.0	0.0	—
7–12	—	—	18.0	—	—	—	2.0	—	—	—	4.0	—	—	—	8.0	—
R82																
1–6	24.6	12.2	1.9	0.0	1.5	0.2	5.1	0.0	3.1	0.0	3.8	0.0	47.7	14.2	2.8	4.2
7–12	—	—	2.7	3.4	—	—	3.8	0.8	—	—	8.0	9.2	—	—	5.7	2.5
R83																
1–6	1.9	1.9	4.1	—	1.9	8.2	15.1	—	14.5	22.9	30.1	—	28.2	27.5	10.3	—
7–12	—	10.9	3.0	—	—	13.0	14.1	—	—	28.3	33.1	—	—	13.1	8.9	—
O82																
1–6	37.0	27.5	5.9	8.3	0.0	7.5	0.0	0.0	11.1	12.5	17.6	4.2	51.8	17.5	5.9	0.0
7–12	—	—	2.6	1.1	—	—	0.0	0.0	—	—	27.2	5.5	—	—	13.2	8.8
13+	—	—	4.4	2.0	—	—	0.0	0.4	—	—	51.4	34.0	—	—	25.2	12.3
W82																
1–6	—	37.1	12.6	—	—	0.0	0.0	—	—	1.6	1.3	—	—	3.2	0.7	—
7–12	—	—	7.5	—	—	—	0.0	—	—	—	2.5	—	—	—	2.5	—
W83																
1–6	—	22.2	6.2	-	—	5.5	6.2	—	—	27.8	8.3	—	—	27.8	25.1	—
	Ectoparasites				*Eurytoma tibialis*				Lepidoptera				Others			

heads to be less attacked. Most of the caterpillars seen were *Eucosma cana* (Haworth) (Lepidoptera: Tortricidae) and damage to heads and the frass produced were easily recognised in the absence of caterpillar. At least one other species was present but unidentified.

The caterpillars feed on the receptacle, achenes and florets. They eat gall tissue where present and may incidentally kill *U. stylata* larvae. Damage by caterpillars was recorded for all heads, with and without galls. It may have been underestimated (in terms of final effects) in the earliest samples, although there was no relationship between proportion of heads damaged and time of sampling.

In general, frequencies of damaged heads increased as head size increased (Fig. 3). Amongst the larger heads, there was no evidence that galled heads were more liable to damage but, in four of the six samples, smaller heads with galls were significantly more liable to damage than those without (Table 14). When *E. cana* infested smaller heads, it appeared to prefer those with galls.

Table 13. Numbers of parasitized *Urophora stylata* L. larvae in different positions in galls. The categories are arbitrary, hence only differences between parasites can be tested. Drawings of galls were not made in B82, and in W82 no *Eurytoma tibialis* were recorded.

Site	Endoparasite *Eurytoma tibialis* Central	Edge	Ectoparasites Central	Edge	X^2 contingency
R82	18	15	2	37	21.7 $p < 0.001$
R83	22	65	0	26	8.2 $p < 0.01$
O82	3	2	10	44	4.5 $p < 0.05$
W83	1	6	4	6	ns trend reversed

Table 14. Percent of heads damaged by Lepidoptera by head size and infestation with *Urophora stylata* L. R = ratio galled: ungalled; p = probability less than given figure (X^2 contingency tables); ns = not significant. (Numbers of heads involved given in Appendix 1.)

Head size	8–19 mm Not galled	Galled	R	p	20+ mm Not galled	Galled	R	p
B82	13.6	25.0	1.8	ns	37.8	60.7	1.6	ns
R82	17.3	24.2	1.4	ns	62.2	67.1	1.1	ns
R83	19.3	42.4	2.2	0.001	88.9	85.5	1.0	ns
O82	14.2	54.8	3.9	0.02	100.0	88.0	0.9	ns
W82	21.5	39.4	1.8	0.05	26.4	38.2	1.4	ns
W83	25.4	73.3	2.9	0.001	47.6	60.0	1.3	ns

As expected, the incidence of damage in gall heads and lepidopteran-caused mortality were correlated (Fig. 4). The relationship appears curvilinear (log transformed slopes > 1), suggesting that when the proportion of heads damaged was high, the amount of damage done to each head (which was not estimated) was also high.

The residual mortality (mostly empty cells and shrivelled larvae) showed broadly the same trends as overall mortality. Although the incidence of this mortality between sites correlated well with lepidopteran-caused deaths, its incidence within sites was different in that buds were usually the worst affected.

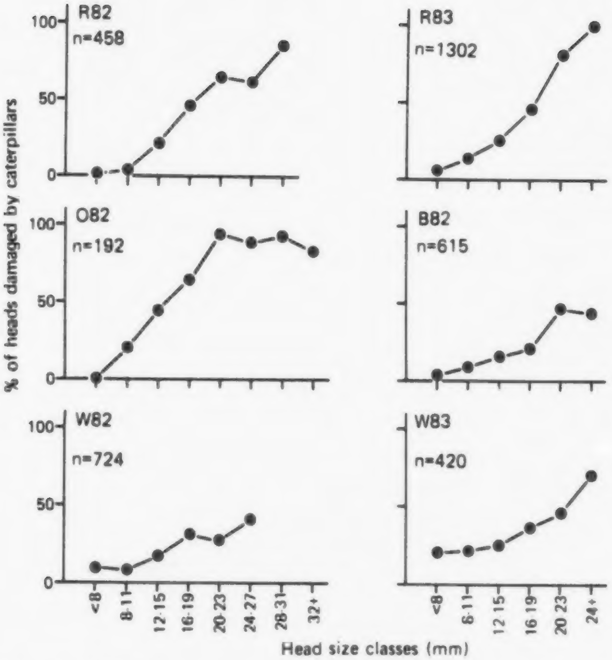

Fig. 3. Percent of heads with lepidopteran damage by size of head (including heads < 8 mm diam. not included elsewhere). Sites as in Fig. 1.

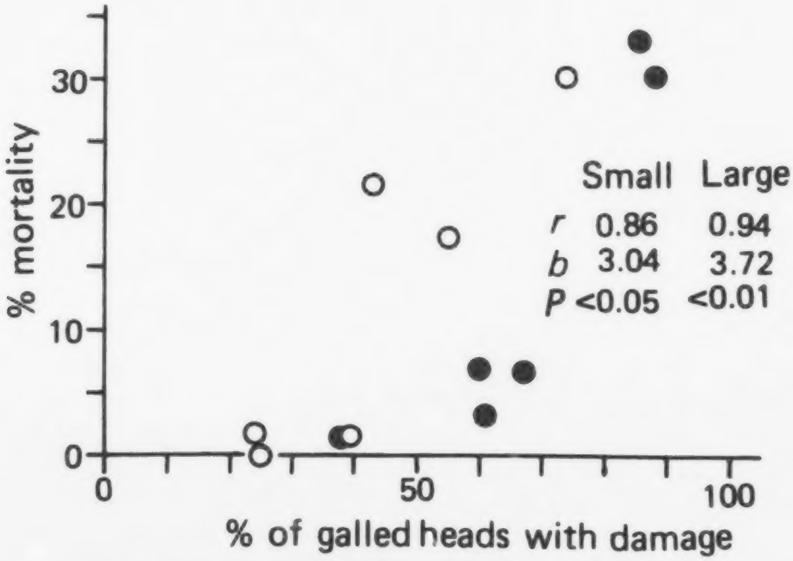

Fig. 4. Percent mortality of *Urophora stylata* L. caused by caterpillars against % of galled heads with lepidopteran damage, for small (8–19 mm, ○) and large (20+ mm, ●) heads.

Discussion

With certain particular exceptions, discussed below, this study revealed clear and consistent patterns of infestation of *C. vulgare* heads by *U. stylata* and demonstrated connections between these and the incidence of larval mortality in *U. stylata*. Before conclusions are drawn, however, it is necessary to consider certain incomplete aspects of this study.

Most importantly, not all the possible factors affecting the likelihood of infestation have been considered. The positions of the heads on the plants were not noted; they are probably related to timing of development and to ultimate sizes achieved but could have an effect on likelihood of infestation independently of those variables.

There is also relatively little information here on the timing of development relative to infestation. Other studies (Varley 1947; Zwölfer 1972; Baloch and Kahn 1973; Berube 1980; Harris 1980*a*, 1984) have shown that oviposition is only successful over a narrow range of bud development both in this species and in other tephritid/composite systems. *U. stylata* adults are, however, present for about two months and it seems that heads developing at most periods within the overall flowering season are at risk of infestation. Only very late-developing buds are free, as in W82 and W83, and observations here and elsewhere (Harris 1984) suggest that mown thistles surviving and flowering late may avoid infestation completely. The proportion of late-flowering heads which set seed is unknown; one could speculate that length and timing of flowering season might be affected in populations subject to persistent and heavy infestation.

In many of our sites, levels of infestation differed between plants and this seems to relate to the mean size of heads. This, in turn, may reflect a diversity in the timing of development between plants which would affect levels of infestation and consequent loss of fertility; that heavy infestation has substantial effects on fertility is well documented (Zwölfer 1972; Harris 1984).

It also seems likely that infestation affects head size. At O82, all the largest heads were infested. In other gall fly/seed head systems, developing galls sequester plant resources (Harris 1980*b*) and it is possible that infestation increases the size of infested heads while reducing the size, and possibly number of, later-developing uninfested heads. The small numbers and large size of heads found at O82 may be a product of heavy infestation. Nevertheless, large uninfested heads occurred at all other sites and it seems unlikely that the difference in mean diameters of infested and uninfested heads was simply a consequence of infestation itself. It is possible, however, that the between-site correlation of mean head size and level of infestation was due, in part, to such a direct effect, a conclusion supported by the higher variability of head size in heavily infested populations.

Attempts to estimate the density of plants in the study areas were not wholly successful. This is a recurrent problem for *C. vulgare*, populations of which tend to be patchy, transient and situated in places (e.g. roadside verges) where orthodox sampling techniques are difficult to apply. There was no evidence in our results of any clear relationship between density (either over a large area or in terms of nearest neighbours) on pattern and level of infestation (Myers and Harris 1980), although other work (Harris 1984) suggests that populations of *C. vulgare* need to be relatively large and persistent to support populations of *U. stylata*. Size of plant (as measured by number of heads) also appeared to be irrelevant to the pattern of infestation, as Harris (1984) also concluded. Both these aspects of host-plant biology need more investigation.

Finally, these studies, by their timing, did not give a complete account of larval and pupal mortality, and some cover a greater span of time than others. In the earliest samples (B82 and R83), ectoparasitism may have been incomplete and, in all but the latest samples (W82 and W83) more damage by Lepidoptera was possible.

These reservations limit our understanding of the causes of patterns of infestation and mortality, but not of their character or consequences. In each site, levels of infestation and numbers of cells/infested head increased with increasing head size. The distribution of cells was clumped, and the greater intensity of infestation of large heads was not simply a product of their greater area.

This selectivity may result from oviposition behaviour or from egg and larval mortality prior to gall formation, or both. Eggs may be laid singly or in small groups (5–10, Persson 1963). Zwölfer (1972) describes the stimuli which determine choice of head by *U. stylata* but there is little evidence on searching strategies of females; in *U. affinis* Frauenfeld, there is no correlation between fly density and *Centaurea* flower head density (Myers and Harris 1980). Likewise, we do not know if female *U. stylata* can detect the presence of other eggs, though the related *U. quadrifasciata* (Meigen) (Varley 1937*a*) and *Tephritis dilacerata* Loew (Berube 1978) apparently cannot. Galls with large numbers of cells are likely to be the product of more than one laying and, since these are frequent, it suggests that *U. stylata* has, at most, very limited powers of detecting earlier oviposition.

There are many accounts indicating that tephritids select particular bud sizes and developmental conditions for oviposition (Varley 1937*a*; Zwölfer 1972, 1977; Myers and Harris 1980; Berube 1980) but it is not clear how these sizes relate, if at all, to achieved size in the fully developed head.

Very little is known of larval competition prior to gall formation. Random laying of clutches will produce a clumped distribution of individuals but, at high levels of infestation, such clumping will be reduced by larval competition. The decline in selection of large heads with increasing levels of infestation seen here suggests that such competition may be occurring, and a decline in clumping at peak densities is recorded for *U. quadrifasciata* on *Centaurea* by Myers and Harris (1980).

Competition before gall formation cannot be a sole explanation of any decline in clumping, since individual heads, even at high intensities of infestation, may have 2–3 times more cells than the mean for their size (maximum of 46 cells in one head at O82). Possible competition after gall formation is considered further below.

Patterns of mortality in these samples have a general resemblance to those recorded for *U. stylata* elsewhere (Redfern 1968; Zwölfer 1972; Cameron and Redfern 1974) and for *U. jaceana* (Varley 1947). Attacks by parasitic Hymenoptera and lepidopteran larvae are the most important causes of mortality between the formation of the gall and the death of the plant. Both overall mortality and that due to particular causes varies considerably between samples. The incidence of mortality appears to be unrelated to levels of infestation, except for that caused by parasites (and particularly ectoparasites), which is heaviest at low levels of infestation. The conclusions of Varley (1947), coupled with the generally higher levels of infestation by *U. stylata* in introduced populations of *C. vulgare* in North America, where parasites are absent (Harris 1984), suggest that parasites regulate the density of *U. stylata*; if so, populations within the natural range must occasionally break through levels within which parasite regulation operates, as seen here at Oberwaiz and Rupertskapelle. At Oberwaiz, levels of infestation matched those seen in introduced populations. Extended studies of populations over several generations are needed to enable firm conclusions to be drawn.

The most important conclusion to be drawn from this study is that risk of dying is not the same for all *U. stylata* larvae. Except in B82 and R83 (sampled early), larvae in buds and small heads had a greater risk of dying than those in large heads and, within the large heads, those at high densities (cells/head) were more at risk than those at low densities. We cannot yet be sure that this non-random distribution of risk is a direct consequence of head size *per se*, as factors such as timing of development and position on plant of the heads may also be important. What we do know is that this distribution of risk matched the distribution of *U. stylata* larvae in the four later samples: larvae were concentrated where the risk of dying is least.

Many studies have investigated the searching behaviour and success rate of insect parasites in relation to the density, distribution and availability of their hosts, and to their own density and mutual interference (Krebs 1978; Hubbard and Cook 1978; Hassell and Anderson 1984). Such studies have often attempted to determine to what extent the parasite is pursuing an 'Optimum Foraging Strategy' which will maximize its success in the prevailing circumstances.

For herbivores such as *U. stylata*, risks of death are arguably as important a determinant of success as the detection and utilization of food. To what extent does *U. stylata* possess an 'Optimum Infestation Strategy'? The evidence here is incomplete, because we do not have data on mortality over the whole life cycle and, in the early samples (B82 and R83), there may have been serious underestimates of several mortality factors. The individual causes of mortality also varied considerably between sites, and each cause had a different pattern of incidence with respect to head size.

The consistent preference for large heads (even when account is taken of area of head available) would appear to be a successful strategy for minimizing attack by ectoparasites and will be, therefore, most successful where this cause of death is greatest, both relatively and absolutely. It appeared to be neutral with respect to attack by *E. tibialis* and counterproductive with respect to attacks by lepidopteran larvae, whose effects were greatest in large heads, especially when number of cells/head was large. The effects of larval competition (before or after gall formation) are at present indeterminate but might also limit the advantage of selective oviposition in large heads, especially at high levels of infestation.

It is worth noting that deaths caused by ectoparasites were the least variable between sites and, therefore, the most predictable over the longer term in which selection for a strategy might operate. Such deaths were also most significant when the levels of infestation were low, which was when the concentration of larvae in large heads was greatest. By contrast, other causes of mortality were more variable between samples and were greatest relative to ectoparasitism in R83, where it appeared that risk of death was the same in all head and gall sizes. The incidence of mortality other than that caused by ectoparasites may explain, therefore, why small heads were also galled; there are circumstances in which it may have been advantageous or, as in R83, in which infestation was optimal in the sense that risk was the same throughout and presumably at an overall minimum.

If such a strategy is innate and unresponsive to short-term fluctuations in causes of mortality, it may limit the usefulness of *U. stylata* as an agent of biological control in areas lacking parasites. Small heads may escape infestation even when there is larval competition in large ones, and seed production will be greater than if larvae were distributed at random (Zwölfer 1972). It will be interesting to see if *U. stylata* modifies its strategy in circumstances, as in North America, in which parasites are absent.

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Appendix 1. Number of buds and developed heads of increasing size infested by *Urophora stylata* L. at six sites. (All plants at each site combined.)

Site		Head size (mm)							
		2–7	8–11	12–15	16–19	20–23	24–27	28–31	32+
Bayreuth 1982									
Buds	No. heads	201	129	96	22	2	1	0	0
	No. galls	0	2	4	1	0	0	7	
	% heads with galls		1.6	4.2	4.5				
	No. cells		2	12	1				
	No. cells/gall		1.00	3.00	1.00				
	No. cells/head		0.02	0.13	0.04				
Developed heads	No. heads	0	10	35	49	55	14	0	0
	No. galls		0	2	8	20	7		
	% heads with galls			5.7	16.3	36.4	50.0		
	No. cells			2	21	91	29		
	No. cells/gall			1.00	2.62	4.55	4.14		
	No. cells/head			0.06	0.43	1.65	2.07		
Rupertskapelle 1982									
Buds	No. heads	124	71	17	0	0	0	0	0
	No. galls	1[1]	27	11					
	% heads with galls	0.8	38.0	64.7					
	No. cells	1	35	30					
	No. cells/gall	1.0	1.30	2.72					
	No. cells/head	0.008	0.49	1.76					
Developed heads	No. heads	0	1	11	43	98	72	21	0
	No. galls		0	5	19	68	58	20	
	% heads with galls			45.5	44.2	69.4	80.6	95.2	
	No. cells			10	39	233	340	156	
	No. cells/gall			2.00	2.05	3.38	5.86	7.80	
	No. cells/head			0.91	0.91	2.35	4.72	7.43	

Rupertskapelle 1983									
Buds	No. heads	323	321	292	19	0	0	0	0
	No. galls	0	11	61	2				
	% heads with galls		3.4	20.9	10.5				
	No. cells		15	82	6				
	No. cells/gall		1.36	1.34	3.00				
	No. cells/head		0.05	0.28	0.32				
Developed heads	No. heads	0	3	117	163	48	16	0	0
	No. galls		1	71	116	42	13		
	% heads with galls		33.3	60.7	71.2	87.5	81.3		
	No. cells		3	120	352	199	101		
	No. cells/gall		3.00	1.69	3.03	4.74	7.77		
	No. cells/head		1.00	1.03	2.16	4.15	6.31		
Oberwalz 1982									
Buds	No. heads	63	13	6	0	0	0	0	0
	No. galls	0	7	4					
	% heads with galls		53.8	66.7					
	No. cells		15	12					
	No. cells/gall		2.14	3.0					
	No. cells/head		1.15	2.0					
Developed heads	No. heads	0	2	10	14	18	25	29	12
	No. galls		2	8	10	16	25	29	12
	% heads with galls		100.0	80.0	71.4	88.9	100.0	100.0	100.0
	No. cells		4	32	35	109	226	404	223
	No. cells/gall		2.00	4.00	3.50	6.81	9.04	13.93	18.58
	No. cells/head		2.00	3.20	2.50	6.05	9.04	13.93	18.58
Waldringfield 1982									
Buds	No. heads	83	45	6	1	0	0	0	0
	No. galls	0	0	0	0				
Developed heads	No. heads	0	29	139	226	153	42	0	0
	No. galls		1	2	30	58	17		
	% heads with galls		3.4	1.4	13.3	24.8	40.5		
	No. cells		2	7	53	109	82		
	No. cells/gall		2.00	3.50	1.77	2.87	4.82		
	No. cells/head		0.07	0.05	0.23	0.71	1.95		

Appendix 1 (continued)

Site		Head size (mm)							
		2–7	8–11	12–15	16–19	20–23	24–27	28–31	32+
Waldringfield 1983									
Buds	No. heads	58	70	20	3	0	0	0	0
	No. galls	0	1	0	0				
	% heads with galls		1.4						
	No. cells		1						
	No. cells/gall		1.00						
	No. cells/head		0.01						
Developed heads	No. heads	0	44	94	95	26	10	0	0
	No. galls		0	5	9	11	4		
	% heads with galls			5.3	9.5	42.3	40.0		
	No. cells			11	34	35	21		
	No. cells/gall			2.20	3.78	3.18	5.25		
	No. cells/head			0.12	0.36	1.34	2.10		

[1] This gall is omitted from all analyses.

Appendix 2. Infestation of thistle heads (buds + developed heads) and survival and mortality (numbers) of *Urophora stylata* L. (*Us*) in heads of increasing size (mm).

Head diameter (mm)	No. heads	Galled heads		Cells/gall		Cells/head	No. cells	No. *Us* survived	No. parasitized by[1]					No. killed by	
		No.	%	No.	± SE				Total	*Et*	*Pe*	*Tc*	*Er*	Lep.	Other
Bayreuth 1982 10 August															
2–7	201	0	0		—	—	0	—	—	—	—	—	—	—	—
8–11	139	2	1.4		—	0.01	2	2	0	0	0	0	0	0	0
12–15	131	6	4.6	2.33	1.81	0.14	14	12	2	0	0	1	1	0	0
16–19	71	9	12.7	2.44	0.56	0.31	22	15	7	4	0	2	1	0	0
20–23	57	20	35.1	4.55	0.61	1.59	91	70	15	1	0	11	3	2	4
24–28	16	8	46.6	4.14		1.93	29	26	1	1	0	0	0	2	0
Rupertskapelle 1982 27 August															
2–7	124	1	0.8	1	—	0.008	1	—	—	—	—	—	—	—	—
8–11	72	27	37.5	1.30	0.13	0.49	35	11	10	0	2	8	0	1	13
12–15	28	16	57.1	2.50	0.32	1.43	38	15	10	1	1	8	0	1	12
16–19	43	19	44.2	2.05	0.25	0.91	39	27	7	4	1	2	0	0	5
20–23	98	68	69.4	3.38	0.45	2.35	233	180	21	15	1	5	0	19	13
24–27	72	58	80.6	5.86	0.36	4.72	340	294	18	11	2	5	0	14	14
28–32	21	20	95.2	7.80	0.70	7.43	156	130	6	2	1	3	0	16	4
Rupertskapelle 1983 14 August															
2–7	323	0	0	0	—	—	—	—	—	—	—	—	—	—	—
8–11	324	12	3.7	1.50	0.23	0.06	18	4	0	—	—	—	—	6	8
12–15	409	132	32.3	1.53		0.49	202	95	11	9	1	0	1	40	56
16–19	182	118	64.8	2.71		1.76	358	141	47	34	3	6	4	80	90
20–23	48	42	87.5	4.73		4.14	199	87	33	27	3	3	0	61	18
24–29	16	13	81.3	7.77		6.31	101	32	22	17	3	2	0	39	8

Appendix 2 (continued)

Head diameter (mm)	No. heads	Galled heads		Cells/gall		Cells/head	No. cells	No. *Us* survived	No. parasitized by[1]					No. killed by	
		No.	%	No. ±	SE				Total	*Et*	*Pe*	*Tc*	*Er*	Lep.	Other
Oberwaiz 1982 27 August															
2–7	63	0	0	—	—	—	—	—	—	—	—	—	—	—	—
8–11	15	9	60.0	2.11	0.42	1.27	19	1	6	0	0.7	5.3	0	2	10
12–15	16	12	75.0	3.67	1.04	2.75	44	15	14	3	2.7	8.3	0	5	10
16–19	14	10	71.4	3.50	0.95	2.50	35	12	9	0	5.4	2.6	1	10	4
20–23	18	16	88.9	6.81	1.28	6.05	109	40	3	0	2.4	0.6	0	28	38
24–27	25	25	100.0	9.04	1.01	9.04	226	107	11	0	3.4	7.6	0	88	20
28–31	29	29	100.0	13.93	1.30	13.93	404	203	9	2	1.4	5.6	0	132	60
32+	12	12	100.0	18.58	3.24	18.58	223	148	6	0	2.4	3.6	0	46	23
Waldringfield 1982 20 November															
2–7	83	0	0	0	—	—	—	—	—	—	—	—	—	—	—
8–11	74	1	1.4	2.00		0.03	2	0	2	0	0	2	0	0	0
12–15	145	2	1.4	3.50		0.05	7	3	3	0	3	0	0	1	0
16–19	227	30	13.2			0.23	53	33	18	0	15	3	0	0	2
20–23	153	38	24.8	2.87		0.71	109	89	19	0	15.8	3.2	0	1	0
24–28	42	17	40.5	4.82		1.95	82	75	3	0	2	1	0	2	2
Waldringfield 1983 22 October															
2–7	58	0	0	—	—	—	—	—	—	—	—	—	—	—	—
8–11	114	1	0.9	1		0.01	1	0	0	0	0	0		1	0
12–15	114	5	4.4	2.20		0.01	11	2	4	0	0	4	0	1	4
16–19	98	9	9.2	3.78		0.35	34	5	7	4	0	3	0	12	10
20–23	26	11	42.3	3.18		1.34	35	16	6	3	0	3	0	1	12
24–29	10	4	40.0	5.25		2.10	21	18	0	0	0	0	0	3	0

[1] *Et* = *Eurytoma tibialis*
Pe = *Pteromalus elevatus*
Tc = *Torymus chloromerus*
Er = *Eurytoma robusta*
Lep. = Lepidoptera larvae

Appendix 3. Survival and mortality (numbers) of *Urophora stylata* L. (*Us*) in relation to number of cells per gall and head size. B = buds, D = developed heads, other abbreviations as in Appendix 2.

Cells/gall	Head diameter (mm)	No. cells	No. *Us*		Deaths caused by					Other
			survived	died	*Et*	*Pe*	*Tc*	*Er*	Lep.	
Bayreuth 1982										
B1–6	8–19	15	13	2	0	0	1	1	0	0
D1–6	8–19	23	16	7	4	0	2	1	0	0
D1–6	20+	70	62	8	1	0	5	0	2	0
D7–12	20+	50	34	16	1	0	6	3	2	4
Rupertskapelle 1982										
B1–6	8–19	65	21	44	1	3	13	0	2	25
D1–6	8–19	49	32	17	4	1	5	0	0	7
D1–6	20–27	312	267	45	16	2	4	0	12	11
D1–6	28+	24	23	1	0	0	0	0	0	1
D7–12	20–27	261	207	54	10	1	6	0	21	16
D7–12	28+	119	100	19	1	1	3	0	11	3
Rupertskapelle 1983										
B1–6	8–19	103	55	48	2	1	0	1	15	29
D1–6	8–19	428	169	259	35	1	6	1	98	118
D1–6	20+	146	59	87	22	4	2	0	44	15
D7–12	8–19	46	16	30	6	2	0	3	13	6
D7–12	20+	135	55	80	19	2	2	0	45	12
Oberwaiz 1982										
B1–6	8–19	27	0	27	0	4	6	0	3	14
D1–6	8–19	40	13	27	3	3	8	0	5	8
D1–6	20–27	85	58	27	0	5		0	15	7
D1–6	28+	24	20	4	0	2		0	1	1
D7–12	20–27	114	63	51	0	3		0	31	17
D7–12	28+	91	76	15	0	1		0	5	9
D13+	20–27	136	26	110	0	6		0	70	34
D13+	28+	512	255	257	2	10		0	174	71
Waldringfield 1982										
D1–6	8–19	62	36	26	0	18	5	0	1	2
D1–6	20+	151	129	22	0	17	2	0	2	1
D7–13	20+	40	35	5	0	1	2	0	1	1
Waldringfield 1983										
D1–6	8–19	36	7	29	2	0	7	0	10	10
D1–6	20+	48	26	22	3	0	3	0	4	12

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Seed Loss Caused by Flower Head Inhabiting Insects of Lesser Burdock (*Arctium minus*)

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Abstract

The insect community inhabiting the flower heads of lesser burdock (*Arctium minus*) growing in Monks Wood NNR, Cambridgeshire, England, was sampled during 1983 as part of a study investigating the effects of competition between the species in use of the food resource. Dissection of dry flower heads collected before seed-fall in September showed that developed seed made up 77.3% of the total seeds in the heads. Of this developed seed, 32.4% was destroyed by insect larvae: 24% by *Orellia tussilaginis*, 3.9% by *Tephritis bardanae* (both Diptera: Tephritidae), 4.9% by *Aethes rubigana* (Lepidoptera: Cochylidae), and 0.3% by *Metzneria lappella* (Lepidoptera: Gelechiidae). Consequently, 50.7% of the total seed crop consisted of germinable seed. Impact of variations in abundance of flowering burdock plants on the populations of these insect species is being studied.

Destruction des Graines par des Insectes Habitant les Capitules de la Bardane Mineure (*Arctium minus*)

La communauté d'insectes habitant les capitules de la bardane mineure (*Arctium minus*) qui croît à Monks Wood NNR, Cambridgeshire, en Angleterre, a fair l'objet d'un prélèvement en 1983 dans le cadre d'une étude portant sur les effets de la compétition entre les espèces pour cette source d'alimentation. La dissection des capitules secs recueillis avant la dissémination des graines en septembre a mis en évidence que 77,3% de toutes les graines des capitules avaient atteint la maturité. Sur ce pourcentage, 32,4% des graines ont été détruites par des larves d'insectes: 24% par *Orellia tussilaginis* et 3,9% par *Tephritis bardanae* (tous les deux diptères: Tephritidae), 4,9% par *Aethes rubigana* (Lépidoptère: Cochylidae), et 3% par *Metzneria lappella* (Lépidoptère: Gelechiidae). Par conséquent, 50,7% de toutes les graines pouvaient atteindre le stade de germination. On étudie actuellement les effets des variations du nombre de bardanes en fleurs sur les populations de ces espèces d'insectes.

Introduction

A major problem in unravelling the relative importance of parasitism and predation on the one hand, and resource limitation and competition on the other, in determining the population numbers of herbivorous insects, is the difficulty in quantifying the food resources available to the herbivore population (Dempster and Pollard 1981). In 1983, work started in Monks Wood, NNR, Cambridgeshire, England, on a three-year study of two tephritid flies (*Orellia tussilaginis* Fab. and *Tephritis bardanae* Schrank; Diptera: Tephritidae) whose larvae feed on the seeds of burdock (*Arctium minus* [Mill] Bernh. and *A. lappa* Linn.; Compositae). Compared to more generalist herbivores, it is relatively easy to quantify the total food supply available to these fly populations, since larval food occurs in discrete units and can be expressed in terms of number of flower heads and seeds produced in Monks Wood each year. Although the main objectives of the study are to determine how changes in the quantity of larval food resources affect the population numbers of the tephritids, with particular emphasis on the role of competition in determining how the flies utilise the food supply, the study also provides an assessment of the impact of seed-feeders on the burdock seed crop and subsequent plant abundance. Data from the first field season in 1983 relating to this aspect of the study are presented here.

Monks Wood comprises 156.8 ha of predominantly oak-ash woodland situated at National Grid Reference TL 50/200800. *A. minus* is common along rides and in other cleared areas where management practices aid the dispersal of seed and provide suitable germination sites. *A. lappa* is not found in Monks Wood, and both species of burdock occur only sporadically in the surrounding arable fields. Although often quoted as being a biennial, burdock plants usually take three or more years to flower under field conditions (Gross and Werner 1983). A single flower stem 25–220 cm tall is produced by a plant during the year in which it flowers, after which the plant dies. The biology of *A. minus* and *A. lappa* is described by Gross *et al.* (1980).

O. tussilaginis and *T. bardanae* are specific to burdock and the larvae gall the seeds inside the flower heads. Adults of *Tephritis* overwinter, and arrive on the flower stems as soon as these appear in June. Eggs are laid into green, unopened buds with a maximum diameter of 11.2 ± 0.5 mm (mean ±S.E.). Larval development is complete by late August and adults emerge in September. *Orellia* appears on buds during July and August, and females select buds 17.4 ± 0.6 mm maximum diameter for oviposition. Since *Tephritis* lays eggs in the field a month earlier than *Orellia*, flower heads chosen by *Tephritis* are also suitable for egg-laying by *Orellia* at the later date. Consequently, larvae of both species are often found in the same flower head. Full grown, third instar *Orellia* larvae overwinter inside single galled seeds, which fall to the ground in September and October. Pupation occurs in the following spring.

Methods

The objectives of the study require construction of life tables for *Orellia* and *Tephritis* for each generation occurring in 1983, 1984, and 1985, together with an adequate measure of availability of burdock flower heads and seeds in Monks Wood each year.

During April–May 1983, Monks Wood was mapped and all flower stems located and numbered. Through summer, additional information was collected on sampled plants, such as maximum height, numbers of flower heads and their stage of development, and subjective assessments of degree of shading and presence of surrounding vegetation. The shade index (*SI*) used ranged from 0 (open canopy directly above plant) to 5 (dense, very low canopy above plant). Although this index cannot describe accurately the specific conditions of light incidence at each site, it is considered that for a large sample of plants it is a reasonable measure of habitat quality.

The distribution of flowering plants was used to design a random sampling programme stratified with respect to high, medium and low plant density. For each flowering plant, the distance to the nearest neighbouring flower stem, and the number of flower stems growing within 25 m were recorded. These two measures were ranked for all plants (values of r_{NN} and r_D respectively) such that a low rank corresponded to a low nearest neighbour distance or large number of adjacent plants. The sum of the squared ranked values $r_{NN}^2 + r_D^2$) was used as a relative measure of plant density. Flowering plants were then ranked on the basis of density and the top third (i.e. those with low r_{NN}^2 and r_D^2 values) taken as high density plants, the bottom third (large $r_{NN}^2 + r_D^2$) as low density plants, and the middle section as medium density. At each sampling occasion, flower heads were taken from plants selected by random numbers, with equal numbers of plants being selected from each of the three density categories.

A series of bi-weekly samples of 102 flower heads taken from 30 plants (10 plants at each density: 5 flowers from different, set positions on 6 plants and 1 apical flower head from 4 plants) was collected from 10 June 1983 to 6 October 1983, frozen, and later dissected to give information on the insect life histories, appearance of developmental stages, and the timing of parasitoid and predator attack. The main insect life table data and information on seed damaged were provided by a bulk sample of 250 flower heads collected 9–15 September 1983, stored dry, and dissected over the winter months. Insect and seed development is largely complete by September and it is possible to analyse the data retrospectively to determine events occurring over the summer period. Larvae of each of the principal seed-feeders attack the seeds in a characteristic manner, hence the number of seeds destroyed by each species can be quantified.

Results and Discussion

I found 2235 flower stems of *A. minus* in Monks Wood during 1983, of which 1780 were used in the sampling programme. The mean number of flower heads produced/plant was 55.3±5.1 (mean ±S.E.) ($n = 199$, August sequential data), with a mean of 39.36±0.84 seeds/head (top apical and mid apical flower heads). Consequently, somewhere in the order of 5.0×10^6 burdock seeds were produced in Monks Wood during 1983.

The overall mean number of heads/plant conceals a considerable amount of inter-plant variation (range: 3–600 heads/plant), which is partly explained by habitat (Fig. 1). Plants growing in open situations ($SI = 0$) produced 89.9±27.8 heads/plant, whereas plants growing in deep shade ($SI = 5$) produced only 19.38±3.67. Low mean numbers of heads/plant at high shade indices result from the combination of two processes: plants are smaller in shady locations; and for a given size, plants under shade produce fewer flower heads than those growing in open situations. Flower heads produce the same number of seeds at each shade index ($SI\,0 = 41.56 \pm 2.92$; $SI\,5 = 40.55 \pm 1.67$). Hawthorn and Hayne (1978) found that *A. minus* in a flood-plain, and presumably highly favourable, habitat in Canada produce 338 heads/plant, but the mean number of seeds/head was the same as reported here.

Twelve insect species have been found inside the flower heads, either feeding on the burdock seeds, or acting as parasites and predators. Besides the two tephritids, caterpillars of *Aethes rubigana* (Treits.) (Lepidoptera: Cochylidae) and *Metzneria lappella* (Linn.) (Lepidoptera: Gelechiidae) consume seeds, but also act as facultative predators on fly larvae. Infestation rates and the numbers of developed seed destroyed/larva of these four primary seed-feeders are given in Table 1.

Developed seed made up 77.3% of the total seed in the dry flower heads before seed-fall in September (unfilled and undeveloped seed = 22.7%; dead seed, 1.5%). Of this developed seed, 32.4% was destroyed by insect larvae; 24.0% by *Orellia*; 3.9% by *Tephritis*; 4.9% by *Aethes*; and 0.3% by *Metzneria*. Consequently, 50.7% of the total seed crop (approximately 2.5×10^6 seeds) consisted of apparently-viable seed. This proportion of viable seed remained constant at high, medium and low plant densities. A slightly greater fraction of seed was damaged by insects at high plant densities (29.5% at high density; 22.2% at low plant density), but this was balanced by a greater proportion of undeveloped seed at low plant densities (19.2% at high density; 27.9% at low plant density). The fraction of seed failing to develop is unlikely to be affected by plant density directly, and an increase at low densities may be due to correlation between the plant density measure and habitat quality.

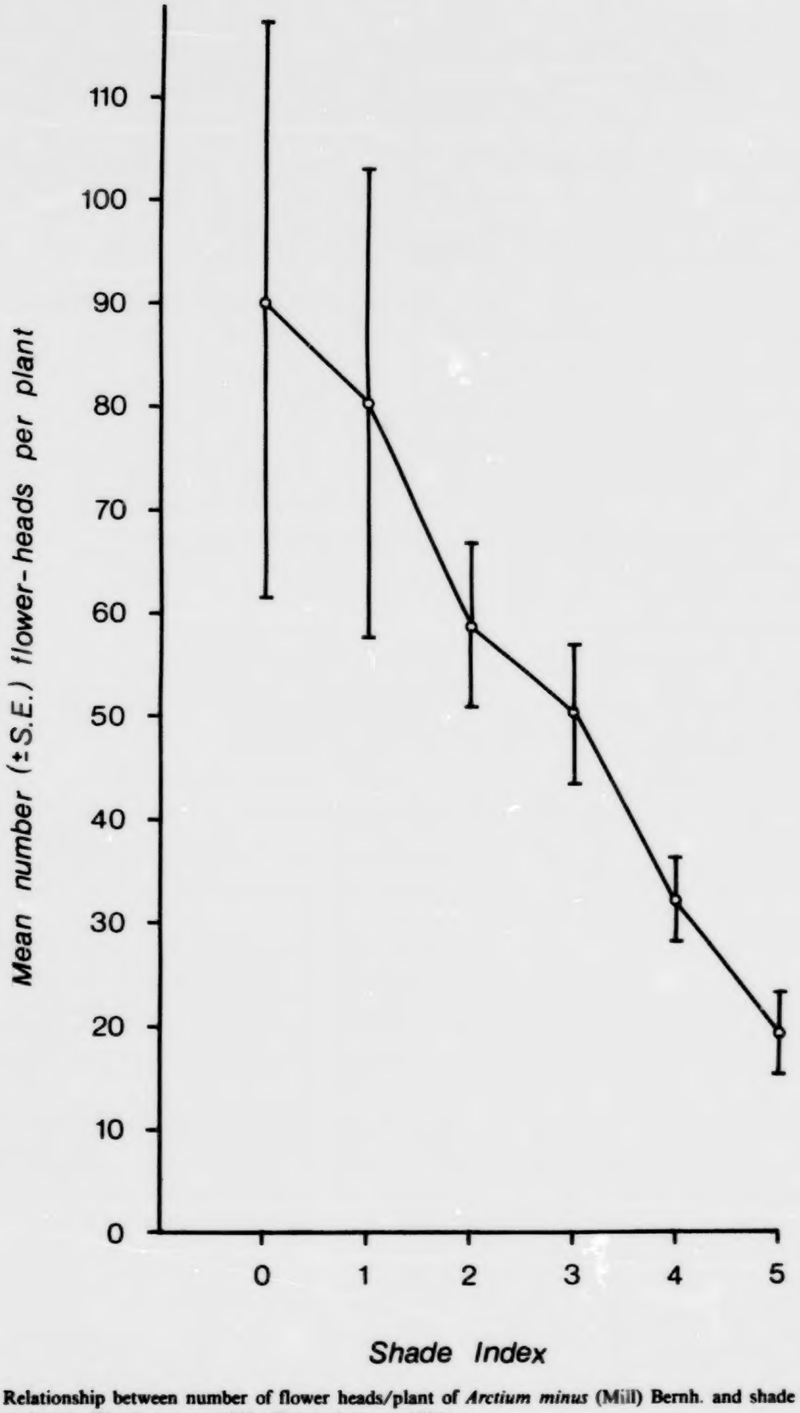

Fig. 1. Relationship between number of flower heads/plant of *Arctium minus* (Mill) Bernh. and shade index (see text), Monks Wood, August 1983. (Total plants = 199.)

The greater proportion of insect-damaged seed at high plant densities resulted mainly from a strong numerical response by *Orellia* to plant density (Table 2). Infestation rates of *Orellia* during 1983 at high, medium and low plant densities were 5.01, 3.40 and 2.37 third instar larvae/head, respectively. In contrast, the total number of seeds damaged by *Tephritis* and *Aethes* was not related to plant density (Table 2). (*Metzneria* was too scarce to analyse meaningfully.)

Table 1. Infestation rates and mean number of developed seeds destroyed/larva of the main seed-feeding species inside flower heads of *Arctium minus* (Hill) Bernh., Monks Wood. (Total flower heads = 250, collected 9–15.ix.83.)

Species	No. larvae/ 100 flower heads	Mean no. developed seeds destroyed/larva
Orellia tussilaginis (Fab.)	363.0	1.92
Tephritis bardanae (Schrank)	27.6	4.06
Aethes rubigana (Treits.)	34.0	3.62
Metzneria lappella (L.)	1.6	5.75

Table 2. Mean number of developed seeds destroyed/flower head of *Arctium minus* (Hill) Bernh. by the principal seed-feeding insects at different plant densities, Monks Wood, 1983.

Species	Plant density		
	High	Medium	Low
Orellia tussilaginis (Fab.)	9.57	6.50	4.57
Tephritis bardanae (Schrank)	0.81	0.22	1.88
Aethes rubigana (Treits.)	1.14	0.74	1.57
Metzneria lappella (L.)	0.04	0.24	0.14
(n = flower heads)	(100)	(50)	(100)

Table 3 gives mean number of developed seeds destroyed/head by the three main seed-feeders and also the average number of seeds damaged/larva of each species, for all flower heads taken from plants growing under different degrees of shade. None of the mean values is significantly different (preliminary analysis using Mann-Whitney U-tests between pairs of samples), reflected by the large standard errors (due mainly to the aggregated distribution of larvae inside flower heads). However, *Orellia* larvae appeared to cause slightly more damage to flower heads from plants growing in conditions of moderate shade (*SI* 2 and 3), as a result of slightly elevated infestation rates. *SI* 2 and 3 contained the greatest proportion of the total plants in Monks Wood during 1983 (0.512 of total plants) and greater numbers of *Orellia* larvae in flower heads taken from these habitats might be expected from the response of the *Orellia* population to plant density. In contrast, the data suggest that *Tephritis* larvae were more abundant in heads from the open sites. Females could simply prefer to lay eggs on buds of exposed plants, but higher infestation rates of *Tephritis* larvae in sunny habitats could derive from an uneven distribution of suitable buds for egg-laying early in the season. *Tephritis* lays eggs into small buds soon after these appear on the stems in June. At this time of year, plants growing in open situations are more advanced than those in shade and provide the majority of oviposition sites. *Orellia* lays eggs a month later when most plants probably bear suitable buds, and adults searching for buds amongst a relatively homogeneous plant population may be more influenced by plant spacing.

Caterpillars of *Aethes* damaged the same number of seeds/head at each *SI*. Slightly higher numbers of larvae at *SI* 0 and 1 appear to be compensated by each larva attacking on average slightly fewer seeds, compared to the smaller number of larvae in flower heads from *SI* 4 and 5. *Aethes* may eat a greater proportion of tephritid larvae at higher plant densities. Alternatively, plants in shade may produce smaller seeds. The figures for the tephritids do not show such a trend, but measurements of puparium sizes suggest that *Orellia* larvae are on average slightly smaller at high shade indices. Clearly, more work on larval food requirements, the interaction of larvae within flower heads, and the sizes of seeds produced by plants growing under different conditions of shade is needed before any such relationships can be confirmed.

Table 3. Larvae/head, mean number of developed seeds attacked/head, and seeds damaged/larva for the three commonest seed-feeders in flower heads of *Arctium minus* (Hill) Bernh. growing under different conditions of shade.[1]

	Shade Index			
	0–1	2	3	4–5
Orellia tussilaginis (Fab.)				
No. third instars/head	2.84±0.71	3.15±0.78	4.47±0.72	2.66±0.82
No. developed seed damaged/head	5.72±1.43	6.10±1.40	8.58±1.25	5.07±1.63
Seeds attacked/larva	2.06±0.11	2.20±0.14	1.96±0.11	2.02±0.15
Tephritis bardanae (Schrank)				
No. third instars/head	0.72±0.30	0.33±0.13	0.27±0.13	0.24±0.12
No. developed seed damaged/head	3.16±1.28	1.28±0.51	1.27±0.62	1.00±0.50
Seeds attacked/larva	4.73±0.38	4.06±0.31	4.90±0.47	4.50±1.04
Aethes rubigana (Treits.)				
No. caterpillars/head	0.56±0.16	0.38±0.10	0.44±0.12	0.38±0.10
No. developed seed damaged/head	1.56±0.58	1.30±0.40	1.56±0.54	1.55±0.47
Seeds attacked/larva	2.50±0.52	3.33±0.54	2.71±0.55	4.15±0.68
(*n* = flower heads)	(25)	(40)	(45)	(29)

[1] Data from 139 top apical and mid apical dry flower heads collected in Monks Wood, 9–15.ix.83; figures given are means ±S.E.).

In 1984 there were < 100 flowering burdock plants in Monks Wood, but adult tephritids were equally, if not more, abundant than in 1983. Dissection of flower heads collected this summer will provide data on how the fly populations have responded to this change in their food supply.

Acknowledgments

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Chapter Six
Biological Control of Aquatic Weeds

Proc. VI Int. Symp. Biol. Contr. Weeds, 19–25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., p. 487 (1985)

The Potential for Biological Control of the Submersed Aquatic Weed, *Hydrilla verticillata*

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Abstract

Since its introduction into the USA 25 years ago, the submersed macrophyte hydrilla (*Hydrilla verticillata*; Hydrocharitaceae) has become one of the most important aquatic pests of the locations where it has become established. A two-year survey of natural enemies of hydrilla in the USA revealed that although some native insect species fed on hydrilla, the damage they caused was not usually significant. Since funding was insufficient to establish and staff an overseas laboratory for searching and testing the natural enemies of hydrilla in its native range, a different approach was followed. For the past three years, I have spent 5–6 months annually in tropical Asia and Australia searching for insects which might be useful in controlling hydrilla. These extensive surveys have resulted in a substantial list of insects damaging hydrilla. The groups which appear to have the greatest potential for being effective biocontrol agents are weevils, especially in the genus *Bagous*; leaf-mining and stem-boring ephydrid flies, primarily in the genus *Hydrellia*; and leaf-feeding aquatic pyralid moths, primarily in the genus *Parapoynx*. Our efforts will now focus on testing these insects overseas sufficiently to allow them to be shipped to quarantine facilities in Florida for more thorough evaluation.

Possibilités de Lutte Biologique Contre la Plante Nuisible Aquatique Submergée *Hydrilla verticillata*

Depuis son introduction aux États-Unis il y a 25 ans, la plante macrophyte submergée, *Hydrilla verticillata* (Hydrocharitacées), est devenue l'une des plus importantes espèces nuisibles aquatiques dans les régions où elle s'est établie. D'après une étude menée durant deux ans sur les ennemis naturels d'*Hydrilla* aux États-Unis, bien que certaines espèces d'insectes indigènes s'en nourrissent, les dommages causés par celles-ci ne sont pas habituellement notables. Depuis trois ans, j'ai passé cinq à six mois par année dans les zones tropicales d'Asie et d'Australie en quête d'insectes qui pourraient être utiles dans la lutte contre *Hydrilla*. Ces recherches approfondies m'ont permis de dresser une importante liste d'insectes qui infestent cette plante. Les groupes qui semblent offrir le plus grand potentiel comme agents efficaces de lutte biologique sont les charançons, particulièrement du genre *Bagous*, les éphydridés mineuses des feuilles et perce-tiges, principalement du genre *Hydrellia*, et les pyrales aquatiques qui mangent les feuilles, principalement du genre *Parapoynx*. Nous procéderons maintenant aux essais qui s'imposent à l'étranger de manière à transporter les insectes dans des installations de quarantaine en Floride où ils feront l'objet d'évaluations plus systématiques.

Proc. VI Int. Symp. Biol. Contr. Weeds, 19–25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., p. 489 (1985)

Evaluation of Grass Carp Variants in Southern California

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Abstract

The aim of this multiagency-funded research project is to evaluate reproductively-incapable versions of the grass carp for use in controlling vegetation (especially hydrilla) in irrigation canals with minimal deleterious impact to the native fauna. Hybrid grass carp controlled vegetation well in 1982 but failed in 1983. Surgically altered grass carp are effective but are more expensive and difficult to insure sterility. Trials of a newly developed triploid grass carp have just begun and initial results are promising, both with regards to vegetation consumption and reproductive inability.

Évaluation de Quatre Espèces de Carpes Herbivores dans le Sud de le Californie

L'objet de ce projet de recherche subventionné par divers organismes est d'évaluer s'il est possible d'utiliser des spécimens stériles de carpes herbivores pour lutter contre la croissance de la végétation (particulièrement hydrilla) dans les canaux d'irrigation tout en minimisant les effets nuisibles sur la faune indigène. Les essais menés avec les carpes herbivores hybrides ont réussi en 1982 mais ont échoué en 1983. Les carpes herbivores sur lesquelles ont été faites des interventions chirurgicales constituent des agents biologiques efficaces, mais cette méthode est plus coûteuse et la stérilité est plus difficile à assurer. Des essais avec des carpes herbivores triploides nouvellement développées viennent de commencer, et les résultats initiaux sont prometteurs, à la fois sur le plan de la lutte contre la végétation et sur le plan de la stérilité.

Proc. VI Int. Symp. Biol. Contr. Weeds, 19–25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 491–6 (1985)

Biological Control of Water Hyacinth on the White Nile, Sudan

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Abstract

First recorded from the Sudan in 1955, water hyacinth rapidly increased to become a major weed. Based on results elsewhere, a biological control program commenced in 1976 with the introduction of *Neochetina eichhorniae*. Under a joint CIBC/ODA/Sudan Government project initiated in 1979, *N. bruchi* and *Sameodes albiguttalis* were introduced and large-scale releases of all species made during 1979–81 resulted in widespread establishment, followed by drastic reduction in the growth rate of water hyacinth. Large floating mats which seasonally covered 113 km^2 behind the Jebel Aulia Dam and required large-scale herbicidal applications, have not appeared since 1982 and chemical control has ceased. The development of the program, its impact on water hyacinth and the economic benefits are discussed.

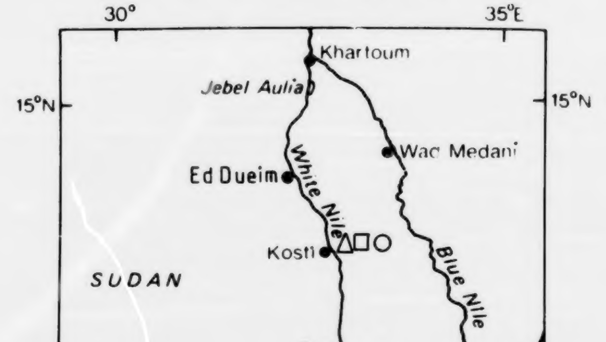
Lutte Biologique Contre la Jacinthe d'Eau dans le Nil Blanc, au Soudan

Depuis qu'elle a été relevée pour la première fois au Soudan en 1958, la jacinthe d'eau s'est rapidement multipliée et est devenue une des principales plantes nuisibles du pays. Un programme de lutte biologique, elaboré à partir des résultats obtenus ailleurs, a commencé en 1976 par l'introduction de *Neochetina eichhorniae*. Dans le cadre d'un projet conjoint mis en oeuvre en 1979 par l'Institut du Commonwealth pour la lutte biologique, l'Overseas Development Administration et le gouvernement du Soudan, *N. bruchi* et *Sameodes albiguttalis* ont été libéré. Grâce à toutes les espèces lâchées sur une grande échelle de 1979 à 1981, les insectes se sont établis sur de très grandes étendues, ce qui a entraîné, par la suite, une réduction très marquée du taux de croissance de la jacinthe d'eau. De vastes tapis flottants qui, en saison, couvraient une superficie de 113 km^2 en amont du barrage de Jebel Aulia et qui nécessitaient l'emploi massif d'herbicides, ne sont pas réapparus depuis 1981, et al lutte chimique a été supprimée. Le rapport traite du déroulement du programme, de ses effets sur la jacinthe d'eau et de ses avantages économiques.

The Problem

The neotropical aquatic weed *Eichhornia crassipes* (Mart.) Solms-Laubach (Pontederiaceae) was recorded from the Sudan in 1955–56 (Heinen and Achmed 1964). First noted as a serious weed in the White Nile system in 1958, it spread rapidly throughout the Sudd region from Juba, over a distance of 1700 km, to the Jebel Aulia 40 km south of Khartoum (Fig. 1). The Jebel Aulia Dam serves as a barrier and with continuous vigilance by the Sudanese authorities, water hyacinth has not established below the dam.

The deleterious effects caused by this weed on the White Nile system are described in detail (Obeid 1975) and include: interference with river transportation including high operational and maintenance costs for ships; blockage of irrigation canals or pumps and access to water for riverine settlements and recreational activities; water loss by evapo-transpiration; fishing losses; and the high cost of chemical control programs. To cope with the problem the Sudanese-Egyptian Joint Nile Committee initiated a control program; the main thrust was based on herbicidal applications by aircraft and launches. As early as 1963 the Plant Protection Division of the Sudan Ministry of Agriculture controlled a fleet of 42 boats and three aircraft and had set up three stations on the Nile to combat this weed. The main purposes of this operation were to maintain open water access for commercial steamer traffic and to riverside villages. In addition to the high annual costs, problems in application created by bad roads and damage to crops by spray drift imposed limitations to this approach.


30°
35°E
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10°
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5°
5°
30°
35°E
Khartoum
Jebel Aulia
Wad Medani
Ed Dueim
White Nile
Kosti
Blue Nile
SUDAN
Renk
Melut
Lake No
Tonga
Khor Wau
Malakal
Bahr el Ghazal
Bahr el Zeraf
Khor Fullus
Sobat R.
ETHIOPIA
Adok
Zeraf Cut
Lake Jur
Shambe
Bahr el Jebel
Bor
Juba
0
100
200
kilometres

Fig. 1. Map of the White Nile system in southern Sudan infested by water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach, showing recovery sites of natural enemies (July 1983). △, *Neochetina eichhorniae* Warner; □, *N. bruchi* Hustache; ○, *Sameodes albiguttalis* (Warren).

The costs of chemical treatment were calculated to be about Sudanese £1 million per annum (Hamdoun and Tigani 1977). Although Philipp *et al.* (1983) gave a lower figure for the earlier years 1964–74, annual costs since 1975 have exceeded this figure.

Biological Control

Background

In 1967, the UK Ministry of Overseas Development (ODM) provided financial support to the Commonwealth Institute of Biological Control (CIBC) to search for natural enemies of water hyacinth in the Neotropics. The objectives were to ascertain the potential and the feasibility of biological control of this aquatic weed in developing countries in Africa, Asia and the Pacific. During surveys in Trinidad, Guyana, Suriname and the Amazon region of Brazil, potential control agents were encountered. These included the weevils *Neochetina eichhorniae* Warner and *N. bruchi* Hustache (Coleoptera: Curculionidae), the lepidopteran stem-borers *Sameodes albiguttalis* (Warren) and *Acigona infusella* (Walker) (both Lepidoptera: Pyralidae), the grasshopper *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae) and the leaf-mining oribatid mite *Orthogalumna terebrantis* Wallwork (Acari: Galumnidae) (Bennett and Zwölfer 1968). These studies overlapped with similar investigations conducted by USDA scientists and local collaborators in Uruguay and Argentina (DeLoach 1975). As a result of these joint efforts, these organisms have been tested and some have been introduced into several countries (Bennett 1983).

Initiation of a Program in the Sudan

The possibilities of biological control in the Sudan were first given serious consideration during a workshop on management and utilization of aquatic weeds in the Sudan and Nile Basin (Obeid 1975). A project proposal was prepared in 1976 (Bennett 1976) and, funded by the ODM, resulted in a joint ODM/Sudan Government project initiated in 1979. In the interim, a program was initiated under the auspices of the Sudanese National Council for Research and, with the cooperation of the USDA, *N. eichhorniae* was imported in December 1976. After further host-specificity trials at the University of Khartoum, releases commenced during May–July 1978.

Construction of a new laboratory facility at the Faculty of Agriculture, University of Khartoum, commenced in 1978, was completed in March 1979 and, under the joint ODM/Sudan project, CIBC obtained *N. bruchi* and *S. albiguttalis* from Florida, again with USDA assistance, during 1979. After further testing, *N. bruchi* was first released in November 1979, and *S. albiguttalis* in 1980 (Fig. 2). For the initial releases of *N. eichhorniae* first instar larvae and eggs were inoculated into the petioles of water hyacinth plants. In the 1979–80 releases, adults, larvae and infested plants were released in sheltered lagoons and side-channels where fairly stable mats persisted for several months, but would eventually disperse and spread the insects throughout the Nile system.

Establishment

N. eichhorniae was first recovered from one of the release sites near Malakal in January 1980 and was reported to be widespread by 1981, when it was collected at Jebel Aulia 270 km downstream from the nearest (1978) release point at Kosti.

Establishment of *N. bruchi* was confirmed in April–May 1981 by which time *N. eichhorniae* was present throughout the White Nile System from Bor to Jebel Aulia, a distance of 1700 km (Irving and Beshir 1982).

S. albiguttalis, released only in small numbers at three sites, was first recovered in 1982; by July 1983 it was widely established from the Sobat junction to Kosti and Bor (Fig. 2).

Impact of Control Agents

Insufficient time has lapsed since the introductions to assess the full impact of the three control agents. Although *N. eichhorniae* has been widely established since early 1981, and has probably reached its population peak, the other two agents are still extending their area of distribution and are increasing in density.

There has been no accumulation of floating mats of water hyacinth behind the Jebel Aulia since 1982, in contrast to the large accumulations (up to 11,350 ha [27000 feddans]) which have occurred annually since the early 1960s and seasonally required constant herbicide treatment.

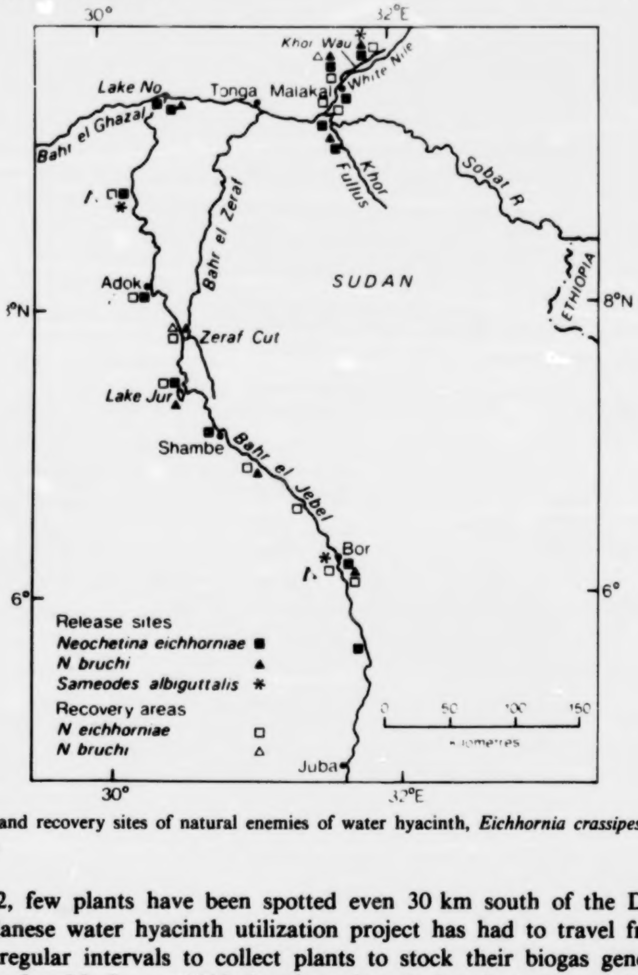
30°
32°E
Khor Wau
White Nile
Lake No
Tonga
Malakal
Bahr el Ghazal
Sobat R
Khor Fullus
Bahr el Zeraf
SUDAN
ETHIOPIA
Adok
8°N
8°N
Zeraf Cut
Lake Jur
Shambe
Bahr el Jebel
Bor
6°
6°
Release sites
Neochetina eichhorniae ■
N bruchi ▲
Sameodes albiguttalis *
Recovery areas
N eichhorniae □
N bruchi △
0 50 100 150
Kilometres
Juba
30°
32°E

Fig. 2. Release and recovery sites of natural enemies of water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach (1981).

Since 1982, few plants have been spotted even 30 km south of the Dam and the German Sudanese water hyacinth utilization project has had to travel from Taweela to Kosti at regular intervals to collect plants to stock their biogas generators. This contrasts sharply with the pre-1982 situation when during the 'south wind period' from May–October, 4–60 ha/day, and between November and April, 30–140 ha/day, originating from the southern regions and out of the Khor, accumulated along the banks at Taweela (Philipp *et al.* 1983). The Plant Protection Division of the Ministry of Agriculture has relaxed its control campaign and the costs of chemical control have been reduced drastically. The intensity of the chemical control program had already started to decline because of financial constraints and deterioration of equipment; hence the reduction in annual biomass of water hyacinth following the establishment of natural enemies occurred at a time when the pressure of herbicide control had been relaxed.

Throughout the area the leaves of virtually every water hyacinth plant are scarred by the feeding marks of *Neochetina* adults, plants are much less vigorous, have a lower dry weight, float lower in the water, and no longer form suitable colonization sites for other plants which previously formed substantial islands on the floating platform provided by healthy water hyacinth plants.

Discussion

The rise and decline of water hyacinth on the White Nile has offered a unique opportunity to assess the impact of water hyacinth, and also the effect that control agents may have on a large river system which is only marginally affected by eutrophication as a result of agriculture or industry.

Hydrobiological research in the Sudan commenced in earnest when a Hydrobiological Research Unit was set up at the University of Khartoum in 1953, although a vast amount of hydrological data, some of it dating back to 660 AD and earlier periods, had been accumulated. Although the construction of the Jebel Aulia Dam in 1936 undoubtedly altered the ecology, there was ample opportunity for the system to stabilize. The hydrobiological data, taken from 1954 until the build-up of water hyacinth commenced in earnest *c.* 1958 (Gay 1958), provided baseline data to permit comparison of data obtained on subsequent surveys.

In preparation for the biological control program, a survey of the fauna and flora associated with water hyacinth on the Sudan was carried out in March 1976. Dr. B. David Perkins, USDA, sponsored by the Sudanese German Water Hyacinth Control Project and one of us (MB) collected data on plant populations, plant size and weight, etc. The Sudanese National Council for Research and the University of Khartoum have obtained similar data on semi-annual survey trips from Juba to Kosti. Similarly, the Sudanese German Water Hyacinth Utilization Project has amassed data on biomass, utilization and control of water hyacinth (Philipp *et al.* 1983).

Hence with the pre-release data and the on-going collection of data, it should be possible in the future to document fully this outstanding example of biological control of an aquatic weed.

It is also too early to evaluate the impact of each of the three introduced control agents. However, the drastic reduction in the amount of water hyacinth accumulating at the Jebel Aulia Dam before *N. bruchi* and *S. albiguttalis* became widespread confirms that *N. eichhorniae* alone, as reported in Australia (Wright 1981), can effect a substantial reduction of growth and cause the collapse of floating masses of water hyacinth.

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Proc. VI Int. Symp. Biol. Contr. Weeds, 19–25 August 1984,
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Flight Muscle and Egg Development in Waterhyacinth Weevils

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Abstract

Waterhyacinth weevils (*Neochetina eichhorniae* and *N. bruchi*) overwintering in northern Florida had undeveloped flight muscles. Exposure in the laboratory to temperatures from 21.1–32.2°C stimulated the development of the flight muscles and resorption of eggs. No flight muscles developed at 37.8°C although resorption occurred. Newly emerged *N. eichhorniae* held at 26.7°C developed flight muscles in 50% of the individuals after 13 days compared to 10 days in *N. bruchi*. Field-collected weevils developed muscles in experiments during the summer but the results were more variable than those with the overwintering weevils. The variability appeared to be due to the temporal variation within the population in the numbers of new weevils that had not previously flown. Both flight muscles and eggs were undeveloped in the field population in October. When October weevils were exposed to 26.7°C, they developed eggs but not flight muscles. Weevils tested during December, including weevils caged since October, developed both flight muscles and eggs, however not in the same individuals. Flight muscles and eggs were almost always mutually exclusive. Photoperiod, weevil density in cages, weevil species and sex, source location of weevils and plants, and food quality were tested for their effects on flight muscle development, but most differences were neither significant nor consistent. Treatment of test plants with the herbicide, 2,4-D, stimulated increased flight muscle development during August, but not during late September–October when few new weevils were present.

Le Développement des Muscles de Vol et des Oeufs chez les Charançons de la Jacinthe Aquatique

Les muscles de vol n'étaient pas développés chez les charançons (*Neochetina eichhorniae* et *N. bruchi*) de la jacinthe aquatique, hivernant en Floride du nord. En laboratoire, l'éxposition de ces charançons aux températures de 21.1° a 32.2°C, a stimulé le développement de ces muscles et la résorption des oeufs. A 37.8°C, quoiqu'il y ait eu résorption, aucun muscle de vol ne s'est développé. Chez des charançons d'éclosion récente, tenus à 26.7°C, le développement de ces muscles s'est presenté chez 50% des individus après 13 jours chez *N. eichhorniae*, mais après seulement 10 jours chez *N. bruchi*. Des charançons ramassés en milieu naturel ont développé des muscles au cours d'expériences conduites en été mais les résultats étaient plus variables que chez les charançons hivernants. La variabilité paraît liée à la variation temporelle, à l'intérieur des populations, du nombre de jeunes charançons qui n'avaient pas encore volé. Chez la population naturelle en octobre, les muscles de vol et les oeufs restaient indéveloppés. L'éxposition de ces charançons d'octobre à une temperature de 26.7°C a stimulé le développement des oeufs mais non celui des muscles de vol. Des charançons soumis à des expériences en décembre, y compris des individus en captivité depuis octobre, ont développé des muscles de vol ou des oeufs, selon l'individu. Presque toujours, les muscles de vol et les oeufs, se sont mutuellement exclus. Les effets sur le développement des muscles de vol, de la photopériode, de la densité de charançons en captivité, des espèces, du sexe, de l'origine des insectes et des plantes, et de la qualité de la nourriture ont été recherchés sans que des différences significatives ni concordantes ne se soit rélevées. Des traitments des plantes-hôtes avec l'herbicide 2,4-D ont stimulé le développement des muscles de vol en août, mais non pas depuis la fin de septembre jusqu'en octobre, époque où il n'avait que peu de jeunes charançons.

Introduction

Two species of waterhyacinth weevils from Argentina, *Neochetina eichhorniae* Warner and *N. bruchi* Hustache (Coleoptera: Curculionidae), have been released in the United States for biological control of waterhyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae). Both species are well-established in Florida and, in fact, during the past seven years the senior author has not found a waterhyacinth population near Gainesville without at least *N. eichhorniae* present. Their wide distribution suggests that the weevils are strong fliers. Stark and Goyer (1983) and Center (1982) reported that large numbers of *N. eichhorniae* flew at night to bright lights in Louisiana during July 1980. Weevil flight was also confirmed when small numbers of adults were captured on sticky traps placed above a waterhyacinth mat during field studies near Gainesville in 1981 (Buckingham, unpubl. data). Stark and Goyer (1983) also reported that attempts by researchers to capture weevils at light traps were generally unsuccessful, as were their own attempts to force the weevils to fly. Flight behavior remained an enigma to us until publication of a paper by Muda *et al.* (1981) on flight muscle degeneration and regeneration in the rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), which is in the tribe Bagoini, as is *Neochetina*. The rice water weevil overwintered in leaf litter away from rice fields and had degenerate flight muscles which were regenerated in the spring. The weevils then migrated to the rice fields where they quickly lost the muscles and began to oviposit. The new adults of the next generation developed muscles and either flew to estivo-hibernation sites or to new rice fields where a second generation was produced which then flew to the hibernation sites. The flight muscles degenerated soon after arrival at those sites. Although there were no reports that waterhyacinth weevils hibernated away from waterhyacinth and, indeed no waterhyacinth weevils were recovered from Berlese samples of leaf litter collected near waterhyacinth mats during the winter of 1977 (Buckingham, unpubl. data), the phenomenon of muscle regeneration and degeneration offered a ready explanation for the previous failure of researchers to observe flight in waterhyacinth weevils. Weevils without flight muscles cannot be forced to fly.

Our first dissections of waterhyacinth weevils in October 1981 revealed that all had undeveloped flight muscles. We thus initiated a field study at a small pond in Gainesville to monitor flight muscle development throughout 1982. The percent of weevils with well-developed muscles collected during that study varied throughout the year. We continued the field study during 1983 and initiated laboratory studies in spring to determine the temperature requirements for flight muscle development. The relationship between wing muscles and eggs was also studied. The laboratory studies were expanded to test factors other than temperature when the results of some experiments varied from those expected based upon the initial experiments. The results of our laboratory studies conducted during 1983–84 are reported here. An understanding of the phenomenon of flight muscle development in waterhyacinth weevils is needed if the weevils are to be effectively managed. Mass migrations during which the adults were nuisances at buildings (Stark and Goyer 1983; Center 1982) and during which they fed temporarily on non-host plants near lights (Buckingham, unpubl. data) might have been predicted if the factors affecting flight muscle development had been known.

Methods and Materials

Adults and cocoons were generally hand-collected from plants, although some adults were swept with an insect net from plants at night. All collections were made in Gainesville at three locations: Shady Nook Trailer Park, University of Florida sewage treatment plant, and Lake Alice. Migrating weevils were collected by sweeping grass beneath street lights at night. Adults which were not able to be sexed and identified immediately were held in a refrigerator without light at *c.* 6°C until they could be and experiments could be initiated. Cocoons were held on moist cotton in 30 ml (1 oz) plastic cups covered by plastic lids with a cotton-plugged hole, or on moist cotton in 0.23- or 0.47-*l* cardboard cups covered with plastic lids. These containers were held in the laboratory at 24±1°C or in a temperature cabinet at 27±1°C. Adults were collected from the containers daily. Various test cages were used: 50 dram plastic vials, 0.9-*l* (1 qt) glass jars, 3.8-*l* (1 gal) glass jars, and aluminum screen cages, 28 × 26 × 52 cm (L, W, H), with hinged lids. The vials and jars, capped with nylon organdy, contained a shallow layer of water. Paper towelling provided footholds for the adults. Excised waterhyacinth leaves with their petioles in the water or in cotton-plugged water vials, or complete plants, were provided for food. Experiments were conducted in temperature cabinets at photophases of 16, 12, or 8 h, and at constant (±1°C) temperatures of 11.1, 21.1, 23.9, 26.7, 32.2, 37.8°C, or varying temperatures of 15.6:26.7 and 24.4:30.6°C. Experiments were also conducted in the laboratory, in the refrigerator at *c.* 6°C, in screen cages in outdoor pools at the laboratory, or in screen cages which were floated at the collection sites. Adults were placed in groups in vials and plant material was placed in cages without apparent bias, and then both were randomized to treatments. Adults were killed in 70% isopropanol and held for at least 1 day before dissection, which made the muscles more apparent. A sample was also killed in 70% ethanol for comparison with isopropanol. Dissections were made by crushing the sternum of the adults with closed forceps, which were then allowed to spring open to expose the indirect flight or median dorsal longitudinal (MDL) muscles lying along the tergum. The MDL muscles were chosen for rating because they were not as easily disturbed during dissection as were the dorso-ventral muscles (DV). Although the fully developed DV muscles were obvious immediately upon dissection, the less developed DV muscles were difficult to evaluate because they were often torn apart during dissections. The MDL muscles were subjectively evaluated and placed into three categories: little to no development; moderately developed; and fully developed. The moderately developed and fully developed categories were combined for data analysis. Measurements of samples in these categories were made with a dissecting microscope with an ocular micrometer. Data were analyzed with chi-square or with Fisher's exact test. When numbers in each category were < 30, the 2 × 2 contingency tables constructed by McGuire *et al.* (1967) using Fisher's exact test were used. Differences were considered significant at $p = 0.05$. Data were converted to percents for correlation, for graphing, and for ease of discussion.

Results and Discussion

Dissections

Our three categories of muscle development are illustrated in Fig. 1. There were three distinct bundles of MDL muscles on each side of the midline. These bundles enlarged during development so that when fully developed they appeared to form one mass on each side. However, they remained distinct and could be teased apart easily with a forceps. This development was similar to that described for the rice water weevil by Haizlip and Tugwell (1983) and Matsui *et al.* (1983). The three bundles were of unequal sizes. Usually the bundle along the midline was largest and the center bundle was smallest. Undeveloped muscle bundles were 39–78 μ wide, moderately developed bundles were 56–117 μ wide, and fully developed bundles were 60–175 μ wide. The unseparated mass of the three fully developed bundles was 331–370 μ wide. Although the ranges of widths overlapped, the categories were relatively distinct because the size overlap was usually between the largest bundle of one category and the smallest of the other. The muscle bundles also increased in depth. The depth was not measured but the increase made the developed muscles more distinct than is indicated by a comparison of the widths since their mass increased geometrically. There were no measurable differences in bundle widths between muscles preserved in isopropanol or in ethanol, however those in ethanol broke apart more readily during dissection which would make rapid evaluation difficult. Thus, we recommend isopropanol as a fixative. Surprisingly, few dissections were in the moderately developed category. Apparently the muscles enlarged quickly, perhaps in 1 day or less.

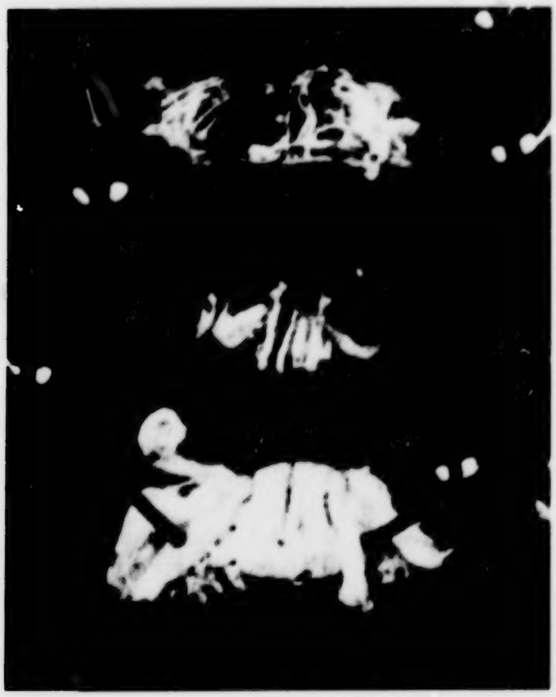

Fig. 1. Three terga of *Neochetina eichhorniae* Warner illustrating undeveloped (upper), moderately developed (center), and fully developed (lower) flight muscles.

Only rarely did a female contain both fully developed eggs and fully developed muscles. Eggs in various stages of disintegration and occasionally dark colored were often present in the ovaries. It appeared that even the contents of eggs with chorions were resorbed. Goldson (1983) reported that he never observed this in the weevil, *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae). As the females switched from egg production to muscle development, they had neither eggs nor developing muscles for a short period. However, in autumn and winter most females collected in the field were in this category. The position of the testes and ovaries in preserved specimens varied with flight muscle development. When the muscles were fully developed and filled most of the thorax, the testes and ovaries were found in the abdomen. When the muscles were not developed, the testes and ovaries extended into the open space in the thorax.

Two interesting observations made during dissections of preserved weevils were that gastric caecae of weevils in some samples were filled with shiny pink colored particles, and that weevils in many samples had internal tissues colored yellowish, along with yellow droplets floating in the blood. If the droplets were lipids as their color suggests, they may have indicated that those weevils were in an active phase of muscle change. The tissues of the majority of preserved weevils were whitish, and there was great variation in the clarity of the body fluids.

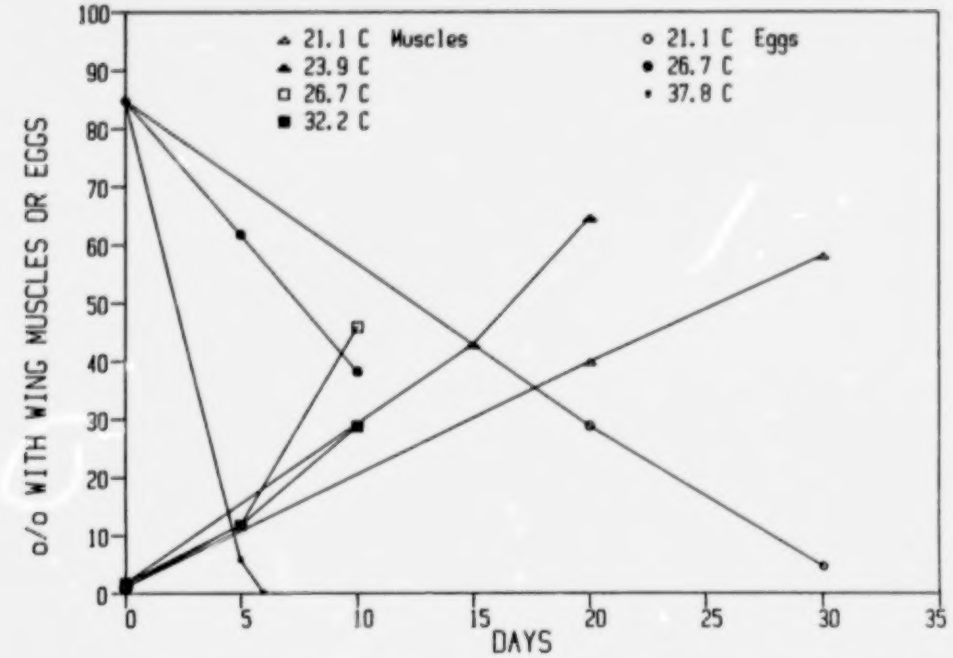

Fig. 2. Development of flight muscles and resorption of eggs in field-collected *Neochetina eichhorniae* Warner tested during May at various constant temperatures.

Temperature

Our initial experiments were conducted during the spring, mostly with field-collected weevils. At the beginning of May only 1% of *N. eichhorniae* and 6% of *N. bruchi* at Shady Nook had developed muscles but 85 and 90% of the females, respectively, were fecund. Sixteen percent of *N. eichhorniae* and 25% of *N. bruchi* at Sewage Plant, where the water was warmer, had developed muscles. The percent of fecund females at Sewage Plant was 75 and 85%, respectively. When both species from both locations were held at various temperatures above 21.1°C, the percent with developed muscles was directly, and the percent of fecund females was inversely, related to temperature and time period. After 15 days at temperatures of 26.7°C or higher, however, there was usually little additional increase in the percent with developed muscles. The May experiment with *N. eichhorniae* (Fig. 2) is representative of the results obtained in experiments from March to June, although the slopes of the lines varied slightly among experiments, especially the 32.2°C line, which was usually steeper at 10 days or less. Only females were held at 37.8°C in the May experiment and they resorbed their eggs rapidly. They had no reciprocal muscle development and mortality at 10 days was 38% compared to 19% for males at 32.2°C, and 5% for both sexes at 26.7°C. Both sexes were tested at 21.1°C, but only males were tested at 23.9°C. The development rate or the reciprocal of the number of days at which 50% of the *N. eichhorniae* had developed muscles (MD_{50}) is plotted in Fig. 3 for the three lower temperatures in the May experiment. If the development rate was also linear below 21.1°C, the lower threshold for development would be about 18.3°C. This threshold may be overestimated as discussed by Wilson and Barnett (1983), but it should still be a helpful guide for future experiments. There was apparently an upper threshold between 32.2 and 37.8°C. Approximations of degree-days for 50% development using 18.3°C as a threshold were 84, 112, and 109 for 21.1, 23.9, and 26.7°C, respectively.

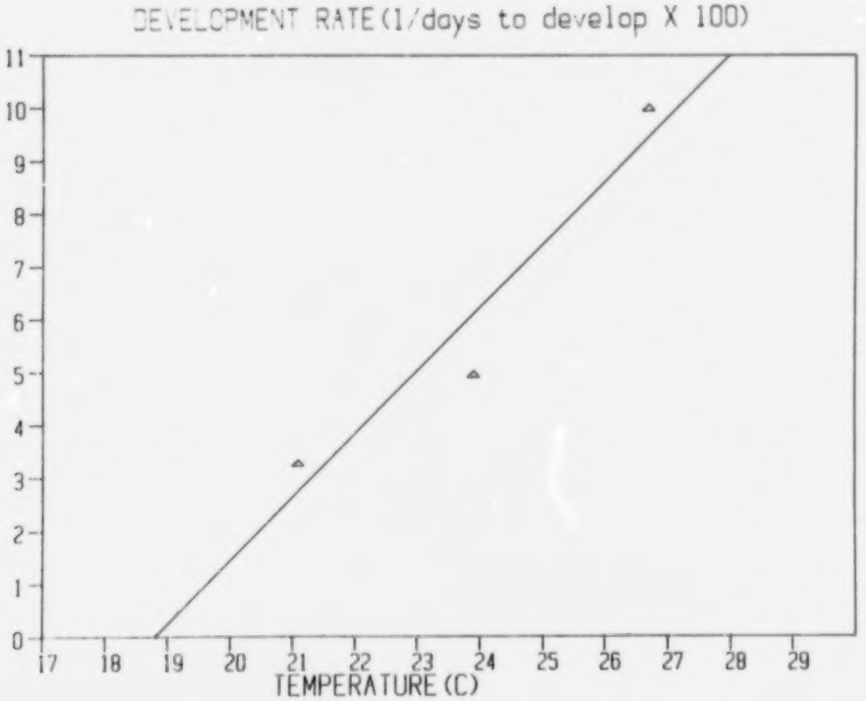

Fig. 3. Development rate for *Neochetina eichhorniae* Warner at three constant temperatures during May. Development of flight muscles in 50% of the weevils.

Weevils that emerged from pupae had both undeveloped flight muscles and undeveloped ovaries at emergence. The MD_{50} for both sexes of *N. eichhorniae* ($n = 46$) tested for 17 days during May at 26.7°C, 16L:8D, was 13 days. Dissections were started at day 5; developed muscles were not found until day 11 in males and day 12 in females. Eggs were found as early as day 7. A larger but still relatively small number ($n = 120$) of *N. bruchi* were also tested for 17 days during May at 26.7°C, 16L:8D (Fig. 4). The MD_{50} for both sexes combined was 10 days. The first developed muscles found in males were on day 6 and in females on day 7. Eggs were found on day 5 in the only female dissected that day. That female is an outlier in Fig. 4. Fourteen of the 34 total males dissected on days 6, 7, and 8 had developed muscles, but only 4 of those 14 had moderately developed muscles. Only one of seven with developed muscles on day 10 was moderately developed, and none had moderately developed muscles after day 10. This illustrated how rapidly the muscles developed once a threshold (?) period was reached (*c.* 50 day-degrees). In many individuals full development apparently required less than a day since we saw no development in one sample and fully developed muscles in the next day's sample. Many females developed eggs initially and then lost them as they switched to flight muscle development. The differences in the development times between the two species may have been a result of different sample sizes, since only nine *N. eichhorniae* had been dissected by day 10 compared to 77 *N. bruchi*. Experiments from January to April with smaller numbers of newly emerged *N. bruchi* held at 26.7:15.6°C, 16L:8D, and 30.6:24.4°C, 16L:8D, produced results similar to the preceding and to those with field-collected weevils. The MD_{50} for the first temperature pair was 28–35 days and for the second, it was < 14 days (MD_{60}). The percent levelled off in both experiments after the MD_{50}, and at 42 days both still had 33% with developed muscles. Most females without developed muscles were fecund.

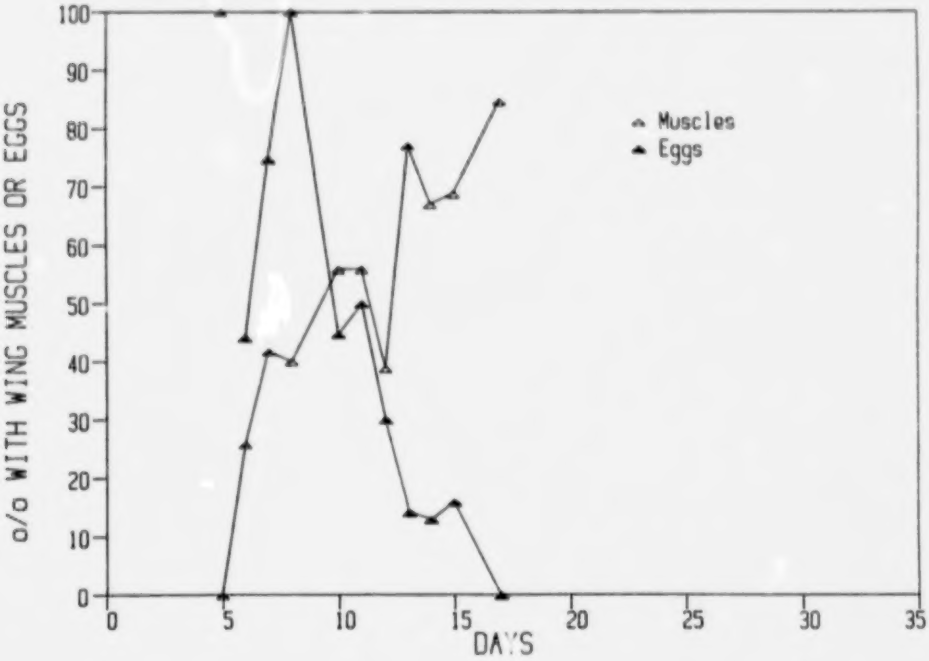

Fig. 4. Development of flight muscles and eggs, and resorption of eggs in newly emerged *Neochetina bruchi* Hustache tested during May at constant 26.7°C.

These experiments with newly emerged *N. bruchi* indicate that at *c.* 26.7°C most individuals developed muscles by day 17. Many began losing them by day 21, but apparently about one-third retained their muscles for at least 42 days. It seems unlikely that some would have developed muscles again soon after losing them, but the possibility cannot be ruled out that the numbers remained constant from 21–42 days not because they retained muscles but because equal numbers regenerated and degenerated muscles. Many females produced eggs before and again after muscle development.

Newly emerged weevils during June, July and especially August developed fewer muscles than in the preceding experiments. For example, only 1 of 29 *N. bruchi* and 1 of 18 *N. eichhorniae* males and females held during July and August at 26.7°C, 16L:8D, and dissected from day 14–22 had developed muscles. Twenty-nine percent of the *N. bruchi* females ($n = 17$) and 54% of the *N. eichhorniae* females ($n = 13$) were fecund. More newly emerged weevils tested during October and November developed muscles than those during the summer, but still less than those during spring. These seasonal differences may have been due to an unknown factor, but we believe that they were due to a change in the temperature at which pupae were held. The spring pupae were held at 23.3°C in the laboratory but the summer and autumn pupae were held at 26.7°C in temperature cabinets. The higher pupal temperature may have stressed them so that most adults were either unable to develop muscles or to develop muscles within the 22-day test period. Most pupae died which demonstrated that they were indeed stressed.

Results with field-collected weevils from June to October were more variable than those in the spring. Although the percent with developed muscles increased somewhat in the majority of experiments, at least initially, it decreased in some experiments. The percent of fecund females increased or remained constant in nine comparisons from July to August, but decreased in 29 comparisons. Five comparisons had increases and five had decreases in September. Muscle development in the field population increased and then decreased during this period, while the percent fecund females decreased then increased. Thus in contrast to the spring, the summer weevils were already highly variable at the initiation of the experiments. Wing muscles and eggs changed inversely in test females. Pearson's correlation coefficient comparing the change in percent flight muscle development and the change in percent fecund for 68 comparisons from March to September with *N. eichhorniae* females was −0.290 ($p = 0.016$). Mortality during the experiments was generally higher during this period compared to spring and especially autumn. Variability in results during summer stimulated us to test other factors, especially those associated with our experimental methods, along with temperature for their effects on muscle development. Those results are reported in a following section.

N. eichhorniae collected in mid-October when the field population had neither muscles nor eggs produced muscles in 5% of the weevils ($n = 39$) and eggs in 11% of the females ($n = 19$) after 7 days at 26.7°C. Only 3% had produced muscles ($n = 30$) at 21 days but 50% of the females had produced eggs ($n = 16$). Weevils collected at the same time were caged outdoors in laboratory pools until mid-December, when they were tested at 26.7°C. At 10 days, 28% had muscles ($n = 40$) and 55% of the females had eggs ($n = 20$); at 21 days, 42% had muscles ($n = 31$) and 63% had eggs ($n = 16$). The percent fecund females did not differ from the October results but the percent with developed muscles was significantly greater in December.

A general increase in flight muscle development was obtained during experiments in December when the field weevils had undeveloped muscles as they did in spring. However, unlike spring when most field females were fecund, the December population had no eggs. The response of these December *N. eichhorniae* to 26.7°C is illustrated in Fig. 5. Both muscles and eggs developed initially, but the percent fecund females peaked at 14 days, and then dropped while muscles continued to increase. At 32.2°C the muscles peaked at 11 days and the percent fecund females continued to increase. Interestingly, similar December experiments during the first year had resulted in little muscle and egg development. Mortality was generally much lower in these winter experiments compared to those in summer.

Pearson's correlation coefficient comparing the change in percent flight muscle development and the change in percent fecund for 19 comparisons during October–February with *N. eichhorniae* females was 0.629 ($p = 0.004$). These comparisons were for 21 days or less and mostly for 14 days or less. A portion of the females produced eggs directly and a portion developed flight muscles. The two conditions were still exclusive.

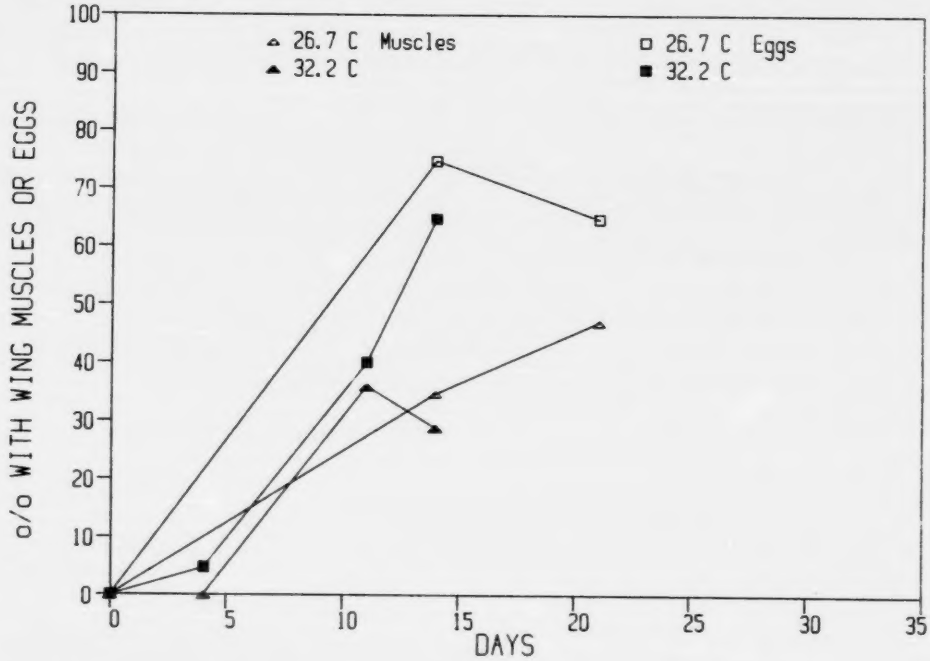

Fig. 5. Development of flight muscles and eggs in field-collected *Neochetina eichhorniae* Warner tested during December at two constant temperatures.

Migrating weevils that were collected beneath street lights at the end of May were tested to observe degeneration of flight muscles. There was no degeneration in *N. eichhorniae* males and *N. bruchi* females after 11 days at 23.3°C, but after 14 days, 27% of *N. bruchi* males and 60% of the females had lost their muscles. Twenty percent of those females had developed eggs after 14 days. There was almost no loss of muscles in *N. bruchi* after 14 days in the refrigerator at 5.6°C. There was greater loss of muscles and reciprocal increase in eggs after 14 days both at 26.7°C and in field cages. *N. eichhorniae* males and females lost 25% of their muscles after 10 days at 32.2°C.

The rapid degeneration of muscles and development of eggs observed in migrating weevils highlights the difficulty of accurately determining the percent change in muscles and eggs after 14 days in summer experiments with field-collected weevils. An observed difference between a final 60% with developed muscles and an initial 20% in the field population might represent a true increase of 40% during the experiment, or an increase of 60% with a concurrent decrease of 20%. However, even if we assume the latter, rarely did 50% of the weevils have developed muscles during the summer experiments.

Other Factors

Experiments were generally conducted with the same species from the same location because of the limited numbers of test insects available at the same time. Ten direct species comparisons were made, however, and differences were significant in only two. In both of those experiments at 26.7°C with Sewage Plant weevils, in January and in July, there was a greater increase in flight muscle development in males of *N. bruchi* than in males of *N. eichhorniae*. In another July experiment at 26.7°C there was a greater increase in flight muscle development in Shady Nook *N. eichhorniae* males than in Sewage Plant males. Although that was the only experiment in which weevils from both locations were compared, weevils from both locations were tested independently in similar experiments which produced similar results.

Differences between the sexes were tested with both species during a total of 72 comparisons that included over 1900 males and 1800 females. Significant differences were found in only four comparisons. *N. bruchi* females had greater flight muscle development in one field cage during July, *N. eichhorniae* females had greater development after both 14 and 21 days at 26.7°C during July, and *N. eichhorniae* males had greater development after 30 days at 23.3°C during February. Various replicates of these four comparisons had no significant differences. The sexes of both species were also compared for the amount of flight muscle loss in migrating weevils. Thirteen comparisons were made with a total of 240 males and 167 females. Only two comparisons were significant, with *N. bruchi* females losing muscles faster after 14 days both at 26.7°C and in field cages.

Various weevil densities were tested for their effects on flight muscle development, but no significant differences were found. Equal weevil numbers were compared in containers of different sizes: 0.9-*l* jars *vs.* 3.8-*l* jars, and 0.9-*l* jars *vs.* 50 dram vials. Varying weevil numbers were also compared in containers of equal size. Wing muscle development occurred at weevil densities as low as 4/0.95-*l* jar and 10/3.8-*l* jar, and as high as 70/0.95-*l* jar in experiments where factors other than density were tested. Even the highest density did not stimulate increased development. No field-collected weevils were caged individually and compared with weevils at other densities; however, newly emerged weevils caged individually did develop wing muscles. It appears that weevil density, by itself, was not an important factor in flight muscle development, although the possibility cannot be ruled out that all densities tested with field-collected weevils were above an unknown threshold density.

Most experiments were conducted with 16-h photophases. However, a few were conducted with shorter photophases. Significant differences were found in only one of the 10 comparisons with a total of 379 field-collected weevils. Wing muscles developed in a greater percent of *N. bruchi* females tested in July with 16-h photophase than with 8-h. The same percent with each photophase lost eggs. In contrast, more *N. eichhorniae* males developed muscles when tested in May (at 12-h rather than with 16-h photophase), but the results were significant with only a one-tailed test. A few newly emerged *N. bruchi* males produced muscles with both 8- and 12-h photophases, and two of nine newly emerged *N. bruchi* females produced them with 12-h. Although photoperiod was not intensively tested, development of muscles at various photoperiods suggests that photoperiod is not important, or at least not a limiting factor in flight muscle development.

Excised leaves, which were used in most experiments because of convenience, and whole plants from the same and different locations, fertilized plants, and herbicide-treated plants were compared in various experiments for their effects on flight muscle development. Over 2200 field-collected weevils were dissected in 26 direct comparisons of plant material. An additional 270 migrating weevils in five comparisons were dissected to observe flight muscle loss. Although field-collected weevils tested on plant material from the Sewage Plant generally had greater flight muscle development than those on Shady Nook material, the differences were neither consistent nor significant. The same was true for comparisons with plant material from Lake Alice and laboratory pools. In one experiment with migrating weevils, there was a significantly greater loss of flight muscles after 14 days in outdoor cages at the laboratory on Shady Nook plants than on Sewage Plant plants. However, there were no consistent or significant differences in other experiments with migrating weevils.

There were also no consistent or significant differences when excised leaves and whole plants from the same location were compared, except in two experiments. More *N. bruchi* females had developed flight muscles during March and April after one month on excised leaves from the Sewage Plant than on whole plants. In contrast, the number of fecund females was significantly greater on the plants. In late May and early June, significantly more *N. eichhorniae* males developed muscles after 10 days on excised leaves from laboratory pools than on whole plants but there was no difference in a companion experiment. No significant difference was found between the numbers of *N. eichhorniae* males and females that developed flight muscles when held for 12 days during July on plants fertilized with a liquid fertilizer than on unfertilized plants, although those on the fertilized plants did develop more muscles. The number of fecund females was greater but not significantly on the unfertilized plants.

Excised leaves of precise ages were not compared but young center leaves, senescing outer leaves, and whole plants were compared using *N. eichhorniae* males during August. There was a significantly greater development of wing muscles in males caged at 26.7°C for 10 days on whole plants from laboratory pools than in males on both young and senescing leaves from Shady Nook. There was no significant difference between the two ages of leaves. There was also no significant difference among the three treatments in companion experiments at 21.1°C for 20 days and at 32.2°C for 4 days and in experiments with females at 32.2°C for 10 and 15 days. Although leaves of mixed ages in good condition were generally used in the experiments, occasionally leaves with heavy weevil feeding, partially dried leaves, and mite-infested leaves were tested. Those leaves did not stimulate unusually high flight muscle development.

Herbicide treatment of waterhyacinth would eliminate the weevils' food supply and force them to either migrate or perish. Thus plants painted with 2,4-D were tested to determine if they stimulated muscle development. There were no differences between painted and unpainted plants with *N. eichhorniae* females in outdoor cages during June and with males and females at 25.7°C during July. However, in both experiments the number with developed muscles increased significantly on both treatments after 14 days. Significantly more *N. eichhorniae* males and females developed flight muscles in August after 14 days on painted plants in field cages at Shady Nook than on unpainted plants. Weevils killed after 7 days on painted plants were not significantly different from those on unpainted plants after 14 days but both were significantly greater than the controls killed at the initiation of the experiment. There were no significant differences in the number of fecund females although there were fewer on the 2,4-D plants at 14 days. Treatments with 2,4-D were tested again in field cages at Shady Nook at the end of September–early October with both *N. eichhorniae* and *N. bruchi*. After 14 days there were no significant increases in flight muscle development on either painted or unpainted plants with either weevil species. In fact, only 5 of 145 total weevils developed muscles. The number of fecund *N. eichhorniae* decreased in both treatments as it did in the field population during that period. The number of fecund *N. bruchi* increased in the control as it did in the field population but there was no increase in the 2,4-D treatment. These experiments indicate that 2,4-D treatments might speed development of flight muscles in new weevils as they did in August, but that they do not stimulate development in weevils (October) that are not already developing muscles. An effect of 2,4-D on speed of development may have been masked in the June and July experiments. Higher water temperatures in the pools and temperature cabinet compared to Shady Nook pond may have stimulated all potential weevils to develop flight muscles by 14 days. Thus effects that occurred before 14 days would have been missed.

Starvation was not extensively tested but migrating weevils retained flight muscles for at least a month in the refrigerator without food. At laboratory or warmer temperatures, flight muscle degeneration in migrating weevils held without food or on non-host plants was similar to that in weevils on the host plant. Newly emerged weevils held without food did not develop flight muscles except possibly once. Seven newly emerged *N. bruchi* apparently developed flight muscles after 9 days in the laboratory without food. That experiment, however, was inconclusive since it could not be repeated.

Conclusions

There are still many unanswered questions about development of flight muscles and eggs in waterhyacinth weevils. However, the general pattern appeared to be similar to that reported for the rice water weevil (Muda *et al.* 1981), except during winter. Waterhyacinth weevil populations overwintered on the host plant and had undeveloped flight muscles but many females were fecund after February, unlike rice water weevil females, which hibernated off the host plant and were not fecund. Wing muscles developed in response to increasing temperatures, and within limits development was directly related to temperature. Females resorbed their eggs, developed muscles which then degenerated, and again formed eggs. Most new females developed eggs before muscles, but some developed muscles directly. The potentially-long adult life span and the long developmental period produce overlapping generations, which were probably responsible for the great deal of variability in summer results. Some field-collected adults in our experiments lived for 31 wks in vials held outdoors from October to July, and Stark and Goyer (1983) reported that the larval and egg development time was about 49 days. Each experiment with field-collected adults would include adults that had already lost their muscles, adults with muscles, and new adults that had not yet developed muscles. The proportion of these would change throughout summer and thus results would vary. Because we did not know the proportion of test weevils that were newly emerged, we were unable to determine if all newly emerged weevils in the field developed muscles or if only some did. Most weevils collected in October had probably already developed and lost their muscles. There were few new adults and thus there was little muscle development in the experiments. The October weevils, however, were able to regenerate muscles in December. This may have been possible because of the two months that had elapsed or perhaps cold weather during late November and December had broken a diapause. The possibility of a diapause is an attractive explanation since weevils tested during the first December did not develop muscles.

The declining condition of the host plant, as illustrated by the 2,4-D experiment, might affect the speed of muscle development in newly emerged weevils, or stimulate a greater percent of newly emerged weevils to develop muscles, but it apparently does not stimulate development in older weevils. Herbicides applied during the summer should be applied when the greatest number of newly emerged weevils are present, if conservation of the weevils is desired. Herbicides should not be applied in spring until the temperature of the water, where weevils rest most of the day, increases above 18°C and allows muscle development. Unfortunately, however, herbicide control is probably more efficient if initiated early in the season, when plants and their populations are small.

This flight-muscle–egg-development pattern may be a general pattern in bagoine and closely related weevils. The senior author has also observed specimens of *Bagous*, *Onychylis*, and *Stenopelmus*, and the tanysphyrine, *Tanysphyrus*, with and without developed flight muscles and eggs. In contrast, the semi-aquatic ceutorhynchine weevils, *Phytobius leucogaster* (Marsham) and *Parenthis vestitus* Dietz, are active fliers when fecund.

The possibility that some waterhyacinth weevils hibernate on shore, as does the rice water weevil, should be more thoroughly investigated. Waterhyacinth, unlike rice, remains during the winter in north Florida, but its populations are greatly reduced. It may thus be of benefit if a portion of the weevils leave the plants. DeLoach and Cordo (1976) reported that waterhyacinth plants were present but greatly reduced in size during winter in Argentina where the weevils originated.

If waterhyacinth weevil populations are to be conserved during chemical control operations, it will helpful to know more about flight muscle development, migration, and egg production. It will also be helpful for an understanding of the biologies of the weevils. Fecundity results that have been reported in several biological studies of *Neochetina* spp. are suspect in light of our results. The authors may have underestimated fecundity by stimulating the weevils to resorb their eggs.

Experiments should be conducted throughout the year with weevils of known age, with plants grown under controlled conditions, with a larger array of temperatures, and with larger numbers of weevils than we tested.

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Leaf Life Tables: A Viable Method for Assessing Sublethal Effects of Herbivory on Waterhyacinth Shoots

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Abstract

Natural enemies of waterhyacinth often do not kill the shoots but cause degrees of leaf mortality, although sporadic outbreaks of any of these agents may temporarily cause severe shoot injury. These mortality agents produce distinct spatial patterns of damage within shoots. Only *Sameodes albiguttalis* moth larvae, *Neochetina* spp. weevil adults and larvae, and occasionally environmental factors affect young leaves and destroy meristematic tissue, thereby effectively killing shoots. Most other factors cause superficial injury and usually only to older leaves. Leaf life tables show that damage caused by *S. albiguttalis* and the two species of waterhyacinth weevils results in an overall 34% reduction of leaf longevity. This is usually brought about by the early destruction of young leaves. Thus, even without direct shoot mortality a degree of control is achieved. Damage caused by *S. albiguttalis* larvae is sporadic and therefore of limited effect. That caused by *N. eichhorniae* is constant and effective. Leaf life tables provide an effective method of comparing impact of biological control agents on waterhyacinth when direct mortality of shoots does not occur.

Les Tableaux de Vie de Feuilles Comme Moyen Valable d'Évaluation des Effets Sous-Mortels des Attaques d'Herbivores sur les Pousses de la Jacinthe Aquatique

Il est fréquent que les ennemis naturels de la jacinthe aquatique soient la cause d'une mortalité plus ou moins importante parmi les feuilles sans tuer les pousses, quoique des éruptions sporadiques de ces agents puissent nuire gravement, mais temporairement, aux pousses. Les dommages causés par ces agents sont répartis à l'intérieur des pousses de manière distincte. Ce ne sont que les larves du *Sameodes albiguttalis* (lepidoptère), les adultes et les larves des charançons du genre *Neochetina*, et parfois, des facteurs de l'environnement, qui affectent les jeunes feuilles ou qui détruisent le tissu méristématique, et de ce fait tuent effectivement les pousses. La plupart des autres agents ne causent que du dommage superficiel, et ce en général seulement aux feuilles plus agées. Les tableaux de vie des feuilles de la jacinthe aquatique montrent que le dommage du au *S. albiguttalis* et aux deux charançons, amène une réduction globale de 34% dans la vie des feuilles, ce qui resulte, le plus souvent, de la déstruction précoce des jeunes feuilles. Ainsi, même sans mortalité directe des pousses, on arrive à un contrôle partiel. Le dommage du aux larves du *S. albiguttalis* est sporadique et donc d'un effet limité, mais celui au *N. eichhorniae* est constant et efficace. Les tableaux de vie de feuilles offrent un moyen efficace de comparison entre l'impact des divers agents de la lutte biologique contre la jacinthe aquatique, là où il n'y a pas de mortalité direct des pousses.

Introduction

Life tables (or survivorship tables) have a long history of use in the insurance business for actuarial purposes as a means of computing annuities. Deevey (1947) perhaps first recognized the utility of life tables for analyzing growth of animal populations in nature, although others (e.g. Pearl *et al.* 1941) had earlier applied these techniques to analysis of laboratory populations. Since that time, life table analyses have been used most extensively in animal population biology, especially in the analysis of insect populations.

Harcourt (1969) and Varley and Gradwell (1970) have reviewed the subject in great depth.

Few attempts have been made to study the demographics of plants by way of life table analyses. Notable among these are the studies by Hett and Loucks (1971), Hawksworth (1965), Namkoong and Roberds (1974), and Harcourt (1970). The interested reader should consult the reviews by Harper and White (1974) and Harper (1977). A particularly interesting example from the paper by Harcourt (1970) is his use of crop life tables to assess economic losses resulting from mortality factors by converting population parameters to monetary values. This yields cost-benefit data for pest management practices in agricultural crops. Life tables could be used in weed management to determine the value of mortality factors which affect the target plant. The resultant monetary figures could then be used to compare the cost-benefit of various control approaches.

Two types of life tables are often constructed. The first type is based upon data obtained by observing the successive mortality of individuals in a population as they increase in age. This is the age-specific, horizontal, or dynamic life table. The second type assumes a stable age distribution and is based upon the age structure of the population at a point in time and infers death rates from the decline in numbers of successive age-classes. This is the time-specific, vertical, or static life table. Krebs (1972), Southwood (1975), Dempster (1975), Deevey (1947), and others discuss types of life tables and their limitations and applications.

Life tables generally deal with whole organisms but in the case of waterhyacinth, the whole plant is difficult to study. The individual leaf is a more convenient unit to use in waterhyacinth population studies (Center 1981). There are many advantages of studying leaves. They are identifiable structural units. Leaves are produced singly at the stem apex and at regular intervals, so leaf age structure is determinable. Leaf production occurs at predictable and easily measured rates. Leaves are conspicuous organs and the most obvious feature of the plant. Leaves often comprise the majority of the biomass. Organisms which damage or kill leaves are easily identified. Biological control agents all feed upon or infest the leaves and affect leaf production and turnover. Leaves have a distinct life cycle. Leaves are easily tagged for repeated observation. Leaf age distributions are relatively stable.

The main disadvantage of studying leaves is that the point of death of a leaf is not always clear. A leaf should be considered dead when it is no longer functional. Because the leaf gradually senesces, death must be subjectively determined. Also, the loss of a leaf does not translate directly into reduced productivity or fitness. This is due to many reasons which have recently been reviewed by Crawley (1984). Also, organs other than the leaves may be more vitally important to the plant.

Population studies of waterhyacinth leaves have provided us with a great deal of useful information. The information is limited, however, and more is needed for a proper evaluation. Richards (1934) warned against inference drawn from a static system and applied to a dynamic one in terms of physiological change related to leaf age. A combined approach is necessary. Harvesting studies document changes, but studies of leaf dynamics provide insight into the process of change.

This paper provides examples of data from field studies in which I examine the within-shoot dispersion of various natural enemies on waterhyacinth. It concludes by using some of these data to construct an example of a time-specific life table to show how this technique might be used to compare the impact or importance of mortality factors. The interested reader should refer also to Abul-Fatih and Bazzaz (1980), Carpenter (1980), Nobel *et al.* (1979), Sagar and Mortimer (1976), and Harper (1977, 1981) for other examples and approaches.

Methods and Materials

Studies were conducted at 15 sites in Florida (Fig. 1) during a four-year period. Data are too extensive to be dealt with in detail so only examples will be presented.

Sampling consisted of examining waterhyacinth shoots, classifying the leaves by nodal position to age cohorts, and identifying factors which had damaged leaves. During 1978–80 we simply determined if each leaf on 100 shoots was or was not damaged by each particular agent and expressed the data as relative frequencies. A 100 × 100 cm frame was placed over the waterhyacinth to delimit a sample area. All plants were removed from within the frame and placed in a large plastic bag. Without apparent bias, 10 shoots were randomly withdrawn and examined. This was done 10 times on a transect across the site with samples taken at approximately equal intervals. Later, during 1980–82, the degree of damage done by each agent was estimated based upon percent of leaf area affected. The same general procedure was followed but only four were selected from each sample (40 total). Lamina and petiole were each assumed to represent 50% of the total leaf in this case. Factors which caused separation of the leaf from the shoot were considered to have caused leaf death.

Series of shoots were tagged at some sites to enable re-identification and re-examination. Tags were placed on youngest leaves and live leaves were counted. This enabled estimation of rates of leaf production and leaf death and development of a leaf budget for each shoot. These and untagged shoots were evaluated as described above at approximately monthly intervals. Leaf condition was evaluated based upon percent green and undamaged. Ten to fifteen plants were tagged at each site. Relocating these plants was difficult and time-consuming, but this enabled comparison of spatial and temporal effects.

Results

The spatial arrangement of waterhyacinth leaves is a function of time, so dispersion of leaf injury is also temporal. Patterns of damage varied spatially and depended upon whether leaf damage was random or selective (Figs. 2, 3, 4). If leaf injury was random then degree of damage increased from younger to older leaves and was directly proportional to duration of availability. In this case, both probability of and frequency of attack increased the longer the leaf was available.

If young leaves were selectively attacked then injury carried through, but didn't increase, as leaves aged. No apparent relationship existed between leaf position (or age) and injury intensity. Leaves were susceptible for a short time and then not harmed further.

If mature leaves were selectively attacked, damage sharply increased at one location within the shoot and leveled off thereafter. Rate of increase was dependent upon the degree of preference of the agent and the duration of persistent attack.

These three patterns of leaf injury (random, young leaf preferred, or mature leaf preferred) assume constant herbivore pressure and are basic and over-simplified. Many more complex patterns were observed. For example, some agents preferred certain leaves but not fastidiously so. Agents such as the waterhyacinth moth, *Sameodes albiguttalis* (Warren) (Lepidoptera: Pyralidae), destroyed meristematic tissue which stopped leaf production. Thus, the resultant injury did not carry over to other positions. Other

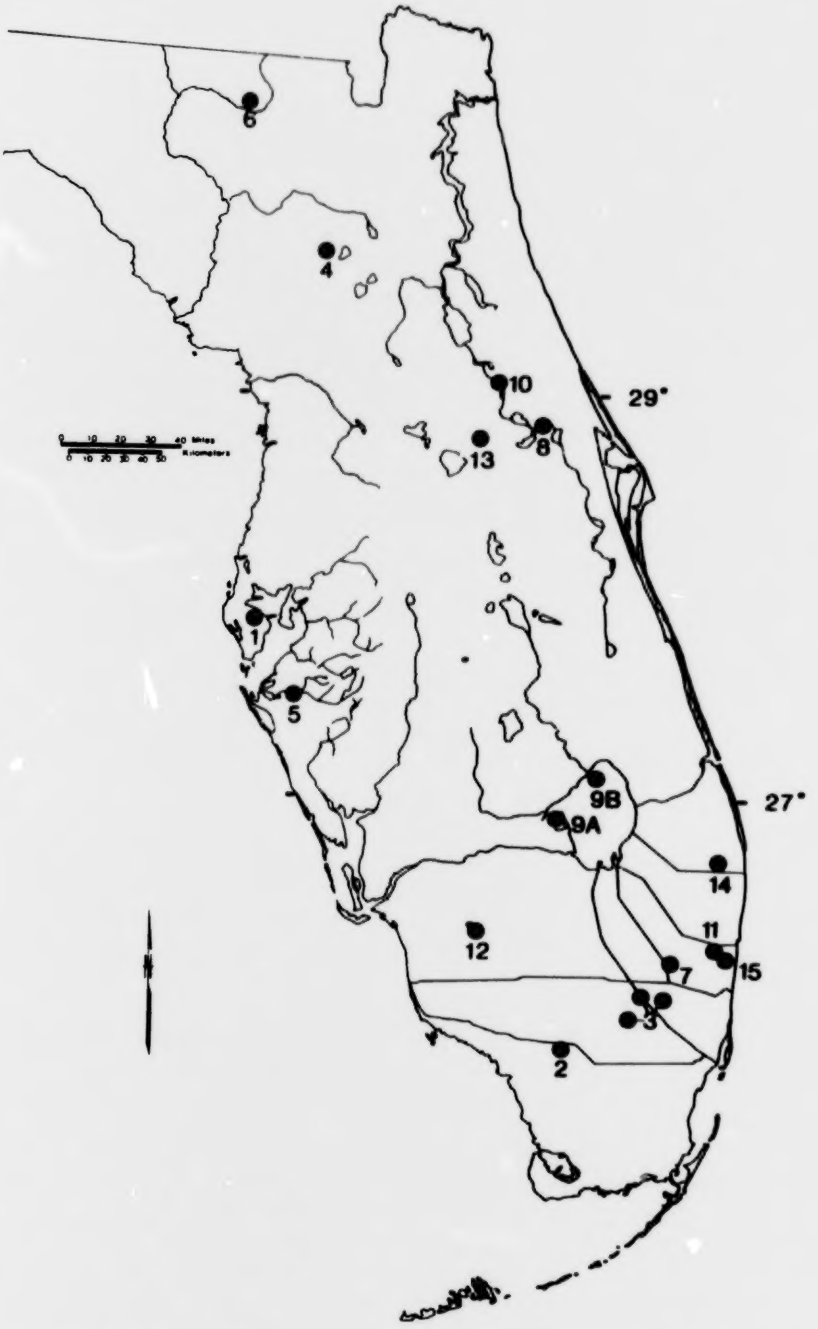
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Fig. 1. The location of the 15 sites in Florida at which data on mortality of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) leaves were obtained between 1978 and 1982.

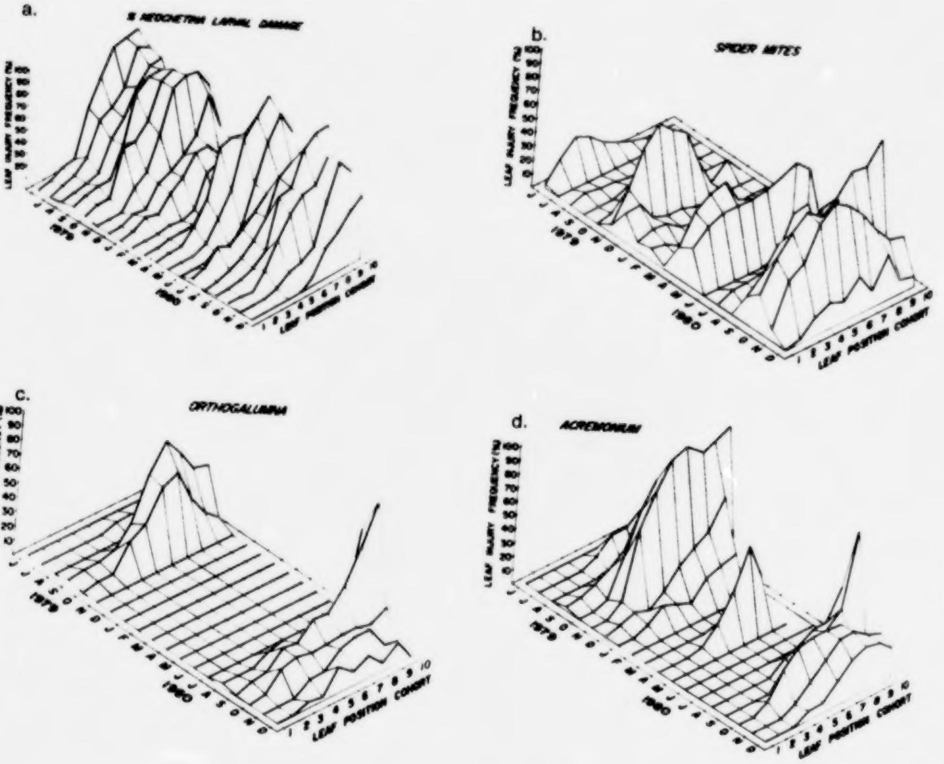

Fig. 2. Data from Lake Alice (site 4), Gainesville, FL, showing the relative frequencies at which leaves of various age classes were damaged or infested by: (a) weevil larvae; (b) spider mites; (c) waterhyacinth mites; and (d) zonate leaf spot disease. Note that spatial patterns of within shoot injury also varied seasonally.

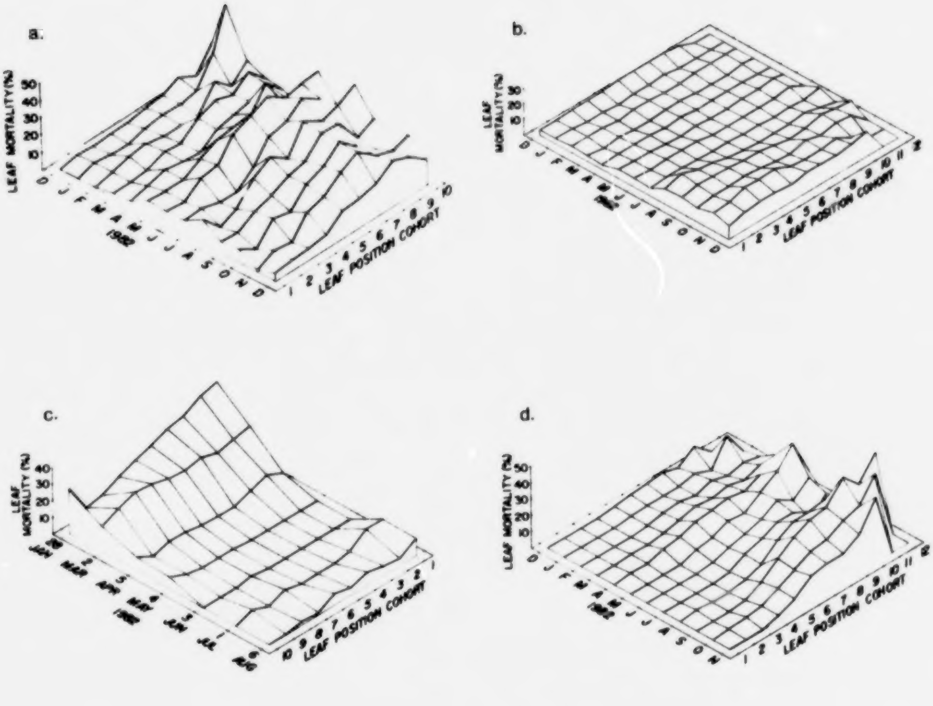

Fig. 3. Data showing the within-shoot spatial dispersion of leaf damage rated according to severity for: (a) weevil larvae; (b) weevil adults; (c) waterhyacinth moth larvae; and (d) zonate leaf spot disease. The leaf cohort axis in Fig. 3c is reversed when compared to the other three graphs. Data for Figs. 3a, b, and d are from Canal-M (site 14), near West Palm Beach, FL. Data for Fig. 3c are from Palm Aire, FL (site 15).

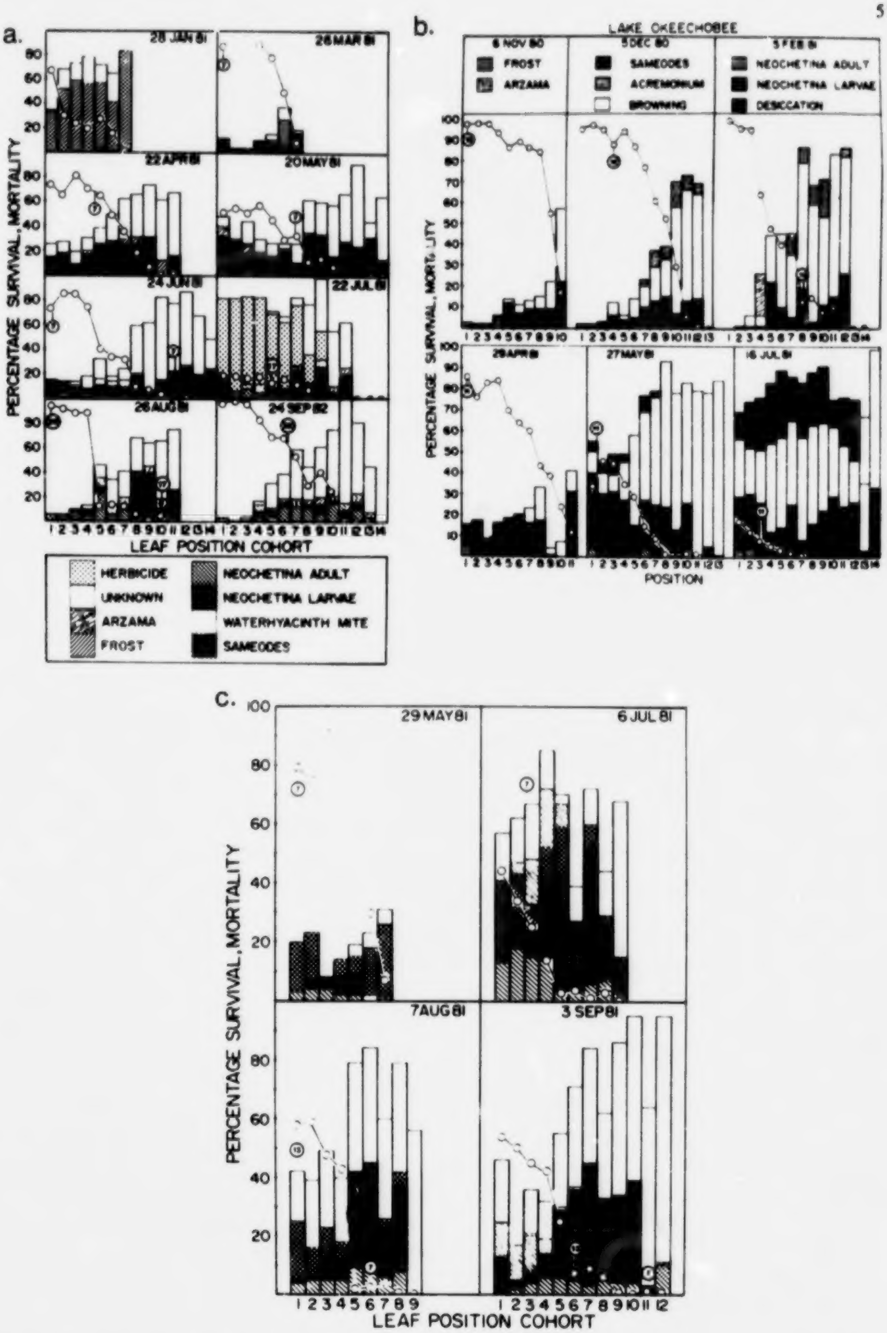

Fig. 4. Data from (a) the Saint John's River (site 10) near DeLand, FL; (b) Lake Okeechobee (site 9); and (c) Coral Springs, FL (site 11), showing relative amounts of damage (bars) caused by various organisms to waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) leaves of varying ages. Dots represent average condition of leaves within each cohort. Small circled numbers show change in leaf position and condition as leaves increase in age. The same number represents the same leaf from one sampling date to the next. The legends in Figs. 4a and 4b also apply to Fig. 4c.

organisms preferred different leaves at different points in their life cycle. Early instar *S. albiguttalis* larvae preferred old leaves, but switched to young leaves as they matured. All exceptions to the basic patterns produced distinct, identifiable patterns, however.

Besides spatial–temporal influence on intra-shoot dispersion of leaf injury, seasonal factors played an important role as did the ability of the plant to outgrow or displace the injury. Seasonal abundance of each organism varied somewhat differently. Leaf production rates varied and were most rapid during the spring. Injured leaves were then replaced more quickly than during fall or winter. Damage appeared lower on the shoot in spring and seemed to 'move up' in fall. Leaves of equal age may have actually been attacked in both cases.

Waterhyacinth weevil (*Neochetina* spp.; Coleoptera: Curculionidae) larvae and adults produced distinctly different injury patterns within waterhyacinth shoots. Eggs are deposited in petioles of a mature leaf (third to fourth position) and hatch in about two wks. The leaf may be displaced two positions (to fifth or sixth) before first instar larvae are present. The larval period requires 30–45 days during which larvae do not readily move out of the original petiole. By then the shoot may have produced five or six leaves. The larva may then be in an old (tenth or eleventh position) leaf before it is large enough to do significant damage. Hence, weevil larval injury usually increased on older leaves. Mature larvae are capable of moving to young leaves. When leaf production slowed, weevil larvae seemed to injure younger leaves (e.g. see Figs. 2a, 3a, and 4c).

Neochetina spp. adults preferred young leaves. The lamina of the youngest leaf was often fed upon while only partially opened. Adults also fed on older leaves but not to the same extent. The resultant pattern of adult weevil injury was indistinct increasing slightly on older leaves (e.g. Fig. 3b) but otherwise with a very low or flat slope over leaf positions.

As mentioned above, *S. albiguttalis* larvae fed on both old leaves or young leaves. When plants were tall, with erect petioles, older leaves were apparently too tough for the larvae. Feeding was then restricted to softer, young, leaves. When the plants were small, early instar larvae fed on older leaves, usually those with soft, spongy, inflated leaf petioles. In this case, as the larvae matured they fed upon young petioles as well. The injury pattern induced by *S. albiguttalis* larval activity was thus variable depending upon plant form and extent of injury. In the former case, especially when the apical bud was destroyed, injury was very high on the first one or two leaf positions and zero thereafter. In the latter case the distribution may have been flat, high on young leaves and increasing on older leaves, or high on old leaves and decreasing on younger leaves (see, for example, Figs. 3c and 4).

The two species of mites produced quite different injury patterns. Spider mites (*Tetranychus tumidus* Banks; Acari: Tetranychidae) occurred in 'boom or bust' population cycles (Fig. 2b). Normally, this species of mite was present in waterhyacinth populations at very low levels. Leaf injury was sporadic and patchy. Occasionally outbreaks occurred and all leaves were affected. Shoots were almost never killed, however, and the outbreaks were generally short-lived. As the plants recovered, the leaf injury was progressively displaced to older leaves.

Waterhyacinth mites (*Orthogalumna terebrantis* Wallwork; Acari: Galumnidae) were never sufficiently common to discern a recurring pattern. They seemed restricted to older leaves (Fig. 2c). These organisms are leaf miners and remain on one leaf through their entire immature period. For this reason they are vulnerable to displacement. Their life cycle requires *c.* 3 wks, during which a waterhyacinth shoot could produce three or four leaves. Galleries were not conspicuous until after the adult emerged. Thus, even if eggs were deposited on young leaves, the injury may not have been apparent until leaves were older.

Zonate leaf spot, *Acremonium zonatum* (Sawada) Gams. (Hyphomycetes), was present at most sites but was usually restricted to old leaves. Figs. 2d, 3d, and 4b show that it was uncommon on younger leaves. When evaluated as to severity, values were usually low and extensive lesions were usually restricted to very old leaves (e.g. Figs. 3 and 4). This is partially related to an association with waterhyacinth mite injury but it also may result from antifungal properties of the leaves (Martyn 1977; Martyn and Freeman 1978). Some data suggest a link between *Acremonium* infection and increased rates of leaf production (Martyn and Freeman 1978) which would accelerate displacement of diseased leaves. In addition, the time involved in lesion development following inoculation may be considerable and the leaves may age considerably before symptoms appear.

Environmental factors such as frosts or droughts impacted waterhyacinth leaves much like spider mites (Fig. 4). They seldom occurred but they affected all leaves. Plants that survived produced new leaves and displaced the injury.

Other factors such as the pickerelweed borer (*Arzama densa* Walker; Lepidoptera: Noctuidae) and the pathogen *Cercospora* spp. (Hypomycetes) were too rare to assess in terms of their spatial distribution on shoots.

Rates of waterhyacinth leaf production varied greatly as shown in Table 1. High rates occurred in flowing systems or in systems with a high nutrient subsidy such as sewage lagoons. The lowest rates occurred when plants were under stress. Seasonally, leaf production rates were highest in spring (Center 1981). Generally speaking, the faster the shoots were able to regenerate damaged leaves, the less the impact of natural enemies.

Discussion

Several parameters are associated with life tables. The parameter x represents the age class or cohort for the interval considered. The number surviving at the beginning of the interval is denoted l_x and the number dying during the interval is denoted d_x. The rate of mortality expressed as the number dying as a proportion of the number entering the age interval is denoted q_x. The parameter T_x is the average number alive per cohort (L_x) summed over all cohorts ($T_x = \Sigma L_x$). The mean expectation for further life for those alive at the beginning of the interval is e_x and is the ratio of T_x/l_x. A specific mortality factor is usually referred to as a function, abbreviated d_xF. In studies of leaves a further parameter must be considered which we will refer to as leaf 'condition' (c_x). An animal cannot be partially dead but a leaf can be. The parameter c_x, therefore, merely represents the average proportion of the individual leaf which remains alive. Therefore l_x represents a value for the number present at the beginning of the interval (n_x) weighted for the average leaf condition (c_x) by deriving the product of the two ($l_x = n_xc_x$). The life table is actually a leaf budget for successive cohorts where losses are ascribed proportionally to various agents of mortality such as insects, disease, frost, etc. Leaf death refers to whole leaf 'equivalents' and may represent a composite of several leaves.

Table 2 presents a time-specific life table for all leaves which were quantitatively examined from the samples of 40 shoots from all sites. This is intended only as an example. Age-specific tables could be constructed in the same manner. Table 3 lists the d_x values for each d_xF on each cohort. Note the number of leaves present (n_x) changed from 870 to 699 from cohorts 6 to 7 indicating a loss of 171 leaves. The leaf

Table 1. Rates of leaf production and leaf death on waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) shoots at several sites. Plants were generally in poor condition at sites with shoots showing large leaf deficits (death rates exceeding leaf production rates).

Site No.	Site	Dates	Time (days)	Leaves/Day Production	Leaves/Day Death	Leaves/Day Difference	Primary Mortality Factor/s
4	Gainesville	10.iii.1981– 7.x.1981	211	0.126	0.098	+0.028	*Neochetina*
6A	White Springs	13.viii.1980– 14.i.1981	154	0.048	0.085	-0.037	*Neochetina*, Frost
6B	White Springs	27.viii.1980– 14.i.1981	141	0.069	0.119	-0.050	*Neochetina*, Frost
6C	White Springs	6.v.1981– 4.xi.1981	173	0.087	0.106	-0.019	*Neochetina*
8	Snake Creek	30.x.1980– 10.xii.1980	40	0.125	0.152	-0.027	Cattle browsing
9A	L. Okeechobee	6.xi.1980– 5.ii.1981	92	0.085	0.135	-0.050	Senescense
9B	L. Okeechobee	29.iv.1981– 16.vii.1981	78	0.021	0.103	-0.082	Drought, *Sameodes*
10	Deland	26.iii.1981– 24.ix.1981	182	0.128	0.127	+0.001	Senescense
11A	Coral Springs	29.v.1981– 3.ix.1981	97	0.075	0.094	-0.019	*Sameodes*
11B	Coral Springs	13.x.1981– 12.xi.1981	30	0.108	0.114	-0.006	*Sameodes*
13	Wekiwa Springs	22.x.1981– 18.xi.1981	27	0.158	0.103	+0.055	None
14	West Palm	23.xii.1981– 30.xii.1982	372	0.114	0.124	-0.010	*Neochetina*
15	Palm Aire	28.i.1982– 6.viii.1982	190	0.150	0.138	+0.012	*Sameodes*

condition (c_x) changed from 49.9% to 38.4% for a loss of 11.5%. Thus $l_x (= n_x c_x)$ changed from 434 to 268. Effects of mortality factors, however, were based only upon c_x and represented cumulative effects. For example, adult weevil feeding accounted for *c.* 8% of the total 71.6% $(1 - c_x)$ deterioration in average leaf condition from cohort 1 to cohort 7. This must be converted in such a manner as to determine effects of weevil feeding upon cohort 6 leaves only. It can be determined that weevil feeding comprised *c.* 10% of the total leaf damage. The change in l_x was a loss of *c.* 77% so weevil damage contributed *c.* 8% to d_x for cohort 6 (i.e. 10% of 77%). Summing these values for all d_xF the total d_x for cohort 6 is 166. Subtracting d_x from l_x yields 268, the l_x for cohort 7. Dividing the l_x for cohort 7 by that for cohort 6 yields the proportion of cohort 6 surviving (S_x) which is 62%. Carrying through the calculations as described earlier, the expected life (e_x) for cohort 6 leaves is an additional 2 leaf positions. In other words, leaves which survive to position 6 can be expected to live to position 8, on average.

Table 2. Time-specific life table analysis for waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) leaf mortality. The data represent averages based on plants collected throughout Florida and during all seasons and, as such, represent a hypothetical 'average' population of leaves.

Leaf Position Cohort (X)	N_x	C_x	l_x	d_x	1000 q_x	e_x	L_x	T_x	S_x
0	1160	1.000	1160	235	202	5.37	1042	5600	1000
1	1160	.797	925	31	34	5.01	910	4558	801
2	1160	.771	894	17	19	4.12	886	3648	783
3	1160	.756	877	134	153	3.41	810	2762	768
4	1118	.665	743	136	183	2.89	675	1952	651
5	1028	.590	607	173	285	2.46	520	1277	532
6	870	.499	434	166	382	2.16	351	757	381
7	699	.384	268	119	444	1.95	208	406	236
8	518	.288	149	70	470	1.74	114	198	131
9	334	.238	79	50	633	1.56	54	84	71
10	187	.154	29	17	586	1.50	20	30	26
11	82	.150	12	9	750	1.25	8	10	7
12	38	.075	3	2	667	1.00	2	2	2
13	10	.090	1	1	1000	0	0	0	1

It should be obvious that leaves are not all equally important to the plant. A leaf must remain healthy to produce photosynthate and thereby contribute to energy demands. Older leaves are less likely to further contribute to the plant and have less remaining life to do so. The importance of a leaf cohort should be proportional to the area under the survivorship curve (Fig. 5) beyond that cohort and this value is equivalent to T_x. If the data represented observations over time this value would be leaf-days but in the time-specific case we will refer to this as leaf-cohort duration.

In theory, the more important biological control agents are those that reduce leaf-cohort duration the most; i.e. those that affect survival of the youngest leaves. In reality, this is not strictly true. The loss of a leaf must also be weighed against the cost of producing it. Loss of an immature leaf may therefore be less important than loss of a mature leaf. Generally, however, damaged immature waterhyacinth leaves continue to develop and are usually not lost. Thus, although considerable function may be lost, the structural cost would be considerable. The loss of leaf area persists for the life of

Table 3. Mortality factors (d_xF) for leaves from Table 2 with contributions of each d_xF to mortality rates of each cohort. Numbers are number dying of the 1160 base populations.

d_xF	Leaf Position Cohort Interval													
	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	Total
S. albiguttalis	136	15	4	25	20	18	11	8	3	3	1	1	0	241
Arzama densa	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Neochetina adult	38	5	3	15	11	11	9	5	3	2	0	0	0	102
Neochetina larva	33	7	5	42	39	45	45	30	15	9	2	1	0	273
Spider mite	4	1	1	4	3	3	2	1	1	0	0	0	0	20
Waterhyacinth mite	0	0	0	5	4	6	5	3	2	1	0	0	0	26
Zonal leaf spot	0	0	0	2	4	9	11	9	6	3	1	0	0	45
Frost	4	1	1	4	6	8	6	2	0	0	0	0	0	32
Partial leaf	0	0	1	11	10	13	10	5	3	3	0	1	0	56
Other	18	2	2	26	38	60	68	56	37	28	10	7	1	353
Total (d_x)[1]	235	31	17	134	135	173	167	119	70	49	14	10	1	1155

[1] Values of d_x may not agree with Table 2 due to rounding error.

the leaf. Further, we have not found compensatory increases in leaf production rates as a plant response to loss of leaf area. Since damage persists through the life of the leaf, agents which attack young leaves reduce leaf-cohort duration, and probably productivity, the most. In the example (Fig. 5) most mortality factors, such as pathogens and mites, affected only old leaves which were near the end of their life expectancy. Introduced biological control insects were essentially the only factors affecting young leaves (i.e. cohort 1). If it is assumed that neither *S. albiguttalis* nor *Neochetina* spp. were present and the life table data recalculated accordingly, the survivorship curve represented by the dotted line in Fig. 5 results. In this case, a new leaf has a life expectancy (e_x) of 7.3 cohort positions whereas otherwise the e_x was 5.4. Leaf cohort duration increased from 5600 to 8467 indicating that the insects account for a 34% reduction even without substantial shoot mortality.

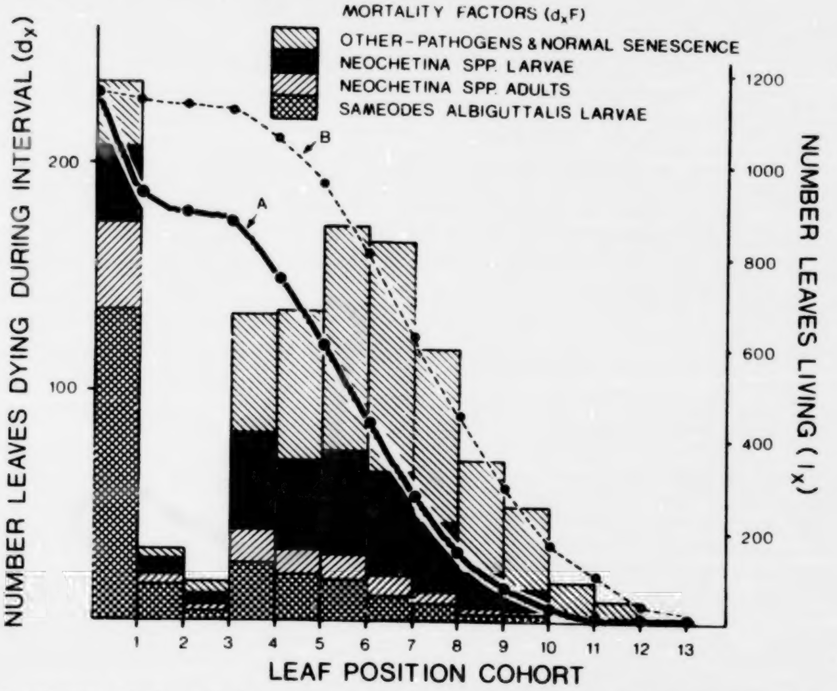

Fig. 5. Life table data from all plants examined from the samples consisting of 40 shoots averaged by leaf position cohorts over all dates and all sites. Line A shows the trend in survivorship (l_x) as leaves age and the bars represent the mortality factors (d_x) responsible for decreasing survivorship. Line B represents calculated survivorship after mathematically removing and re-distributing leaf mortality caused by *Sameodes albiguttalis* (Warren) larvae and *Neochetina* spp. larvae and adults. The result is a 50% increase in survival which indicates that these factors reduce leaf longevity by *c.* 34% primarily through the destruction of young leaves.

Waterhyacinth seems adapted to withstand leaf injury by rapid leaf production thereby soon replacing those injured. The impact of stress on a waterhyacinth shoot depends upon the replacement rate of a damaged leaf relative to the developmental time of the stress factor. Organisms which feed upon or infect leaves, then, are faced with the problem of being able to persist on the shoot. Either their life cycle must be in phase with the leaf's life cycle or they must be able to move to new leaves or other parts of the plants when the leaf dies. The various agents have apparently solved this problem in different ways. For biological control to be effective defensive strategies of the plant must be overcome. Only *S. albiguttalis* and the two weevil species seem to consistently do this.

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The Impact of *Neochetina eichhorniae* (Coleoptera: Curculionidae) on Waterhyacinth in Louisiana

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Abstract

Neochetina eichhorniae was first released in Louisiana during 1974 by the Louisiana Department of Wildlife and Fisheries. This insect species was distributed throughout the State in 1976 and insect populations were well established by 1978. A reduction in waterhyacinth acreage throughout Louisiana occurred. The 1974 population (1.1 million acres) of waterhyacinth in Louisiana was reduced to 301,100 acres by 1980. This four-year study (1980–83) indicated that *N. eichhorniae* effected reductions in waterhyacinth height, density, and biomass at test sites and was a major factor contributing to reduction in waterhyacinth acreage in Louisiana.

Effets de *Neochetina eichhorniae* (Coléoptères: Curculionidés) sur la Jacinthe d'Eau en Louisiane

Neochetina eichhorniae a d'abord été libérée en Louisiane en 1974 par le Department of Wildlife and Fisheries (Departement de la Faune et de la Pêche) de la Louisiane. En 1976, la distribution de cet insecte s'est effectuée dans l'ensemble de l'etat et, en 1978, les populations étaient bien établies. Au fur et à mesure que les populations croissaient, une réduction de l'aire de répartition des jacinthes d'eau a été constatée dans toute la Louisiane. Elle est passée de 1.1 million d'acres en 1974 à 305 000 acres en 1980. D'après notre étude de quatre ans (1980–83), *N. eichhorniae* a causé des diminutions de la hauteur, de la densité et de la biomasse des jacinthes d'eau et a joué un rôle important dans la réduction de la superficie occupée par cette plante nuisible en Louisiane.

Introduction

Waterhyacinth, *Eichhornia crassipes* (Mart.) Solms. (Pontederiaceae), was introduced into the United States at the 1884 Cotton States Exposition in New Orleans, Louisiana, for its decorative inflorescence of blue flowers (Raynes 1964). Since its introduction, waterhyacinth has spread or been distributed throughout a large portion of the United States, particularly in the southeast. Populations have been reported in some western states (Texas to California) and north into Missouri (Godfrey and Wooten 1979). The ability of waterhyacinth to infest a wide range of fresh-water habitats (e.g. lakes, rivers, canals and swamps), and its tremendous growth rate (Penfound and Earle 1948; Center and Spencer 1981) have made it one of the most troublesome aquatic plants in the United States.

Waterhyacinth is capable of both asexual and sexual reproduction. Asexual reproduction, which is more common, occurs by production of vegetatively propagated daughter plants (ramets) that develop on stolons from the parent plant. Once ramets develop, the brittle stolons break and the daughter plants separate from the parent.

Penfound and Earle (1948) reported that 10 plants produced a mat of 655,360 individual plants in one growing season.

Various methods have been employed to control waterhyacinth. Mechanical methods were first employed to prevent downstream movement and to clear navigable waterways. However, chemical spraying with phenoxy herbicides replaced most mechanical operations in the 1950s. Currently, 2-4 dichlorophenoxyacetic acid (2,4-D), a phenoxy herbicide, is the predominant short-term control method employed.

Investigations of biological control began in the early 1960s with researchers exploring areas of South America for candidate biocontrol agents. After 10 years of research, three insect species were identified and approved for use as agents for the biocontrol of waterhyacinth. The first of the three insect species, *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae), was released in Florida in 1972. *N. eichhorniae* was released in Louisiana in 1974 by the Louisiana Department of Wildlife and Fisheries. From 1974–77, 158,000 weevils were dispersed at 492 locations in 39 Louisiana parishes (Manning 1979). *Neochetina bruchi* Hustache and *Sameodes albiguttalis* (Warren) (Lepidoptera: Pyralidae) were released in Louisiana in 1975 and 1979, respectively; however, these species did not become widely distributed.

Both the adult and larval stages of *N. eichhorniae* impact waterhyacinth. Adult feeding on the lamina reduces the epidermal surface area, thereby reducing the amount of photosynthate produced. When feeding is heavy, petioles are often girdled and the laminae become desiccated. Larvae feed on the meristematic tissue in the plant crown. This feeding often separates the growing tip from the rhizome and roots.

The purpose of this report is to document the impact of *N. eichhorniae* on waterhyacinth in Louisiana. This research was one part of a Large-Scale Operations Management Test (LSOMT) (Sanders *et al., in press*) conducted in Louisiana between 1979 and 1983.

Methods and Materials

Four waterhyacinth sites in southern Louisiana were examined during a four-year period. Data from the Assumption Parish and Lake Theriot sites are presented in this paper. Sites were sampled in the spring, summer, and fall of each year, and both plant and insect data were collected.

Assumption Parish

The study at this site was actually designed to test different applications of *Cercospora rodmanii* Conway (Hyphomycetes), a fungal pathogen of waterhyacinth. The *N. eichhorniae* population was monitored to determine its background impact. Twelve 336 m^2 plots were established and *Cercospora* application rates of 4×10^4, 4×10^5, and 4×10^6 Colony Forming Units (CFU)/m^2 were each tested in three randomly assigned plots. The three remaining plots were utilized as controls. Each plot was separated by a distance of 0.6 km (0.4 mile).

The percent of the surface covered by waterhyacinth in each test plot was obtained by averaging the visual estimate of three observers prior to sampling. All data were taken from waterhyacinth plants collected from four randomly-located, 0.25 m^2 (0.5×0.5 m) quadrats in each test plot, and samples were placed in plastic bags until examination. Height of the centermost plant in each quadrat was recorded prior to removal of the plants from the quadrat. Plants from each quadrat were placed in a wire basket, allowed to drain for 1 min., and weighed to the nearest gram. The number of mature plants and daughter plants was recorded separately for each quadrat.

Comparisons (Analysis of Variance, GLM, and Duncan's Multiple-Range Test; SAS Institute Inc. 1982) were made for density, biomass, height, and number of daughter plants between plots for each sampling date. Weighted mean values (no./m^2 × % cover) for density and biomass were calculated for each sampling date, and weighted means were then subjected to the above comparisons.

Five waterhyacinth plants from each quadrat were randomly-selected for assessing pathogen damage. Average pathogen damage/leaf in each quadrat was calculated by summing disease index values (Sanders *et al.*, *in press*) for all leaves on each of five plants and dividing by the total number of leaves. Plot means were determined by summing quadrat means and dividing by the number (four) of quadrats. Mean pathogen damage/test plot was averaged across treatment plots for each sampling date. ANOVA was used to determine whether pathogen damage differed significantly among treatments and sampling trips. Leaf tissue was collected on each sampling trip from selected plants for laboratory re-isolation of *Cercospora*.

The five plants used for assessing pathogen damage were examined for *Neochetina* adults and larvae, and other arthropod species. Mean numbers of *Neochetina* adults and larvae/m^2 were calculated for each quadrat. Resulting means were averaged for each plot and among plots for each sampling trip. ANOVA was used to determine whether mean numbers of *Neochetina* adults and larvae/plant and quadrat varied significantly among sampling trips.

All test plots were sampled in May 1980 prior to application of the formulation. Post-treatment sampling was conducted on 12 July and 30 September 1980. Sampling was discontinued after September due to insufficient numbers of waterhyacinth plants in test plots to obtain valid samples.

Lake Theriot

This site was used to evaluate the impact of *N. eichhorniae*, *S. albiguttalis*, and *C. rodmanii* on waterhyacinth. The site, located in Terrebonne Parish, covered 1.82 ha (4.5 acres). *S. albiguttalis* was released at the site in May 1979 (10,000 eggs) and in June 1980 (1000 eggs). *C. rodmanii* was applied to the site by fixed-wing aircraft on 8 May 1980 at a rate of 35.7 lbs/acre (1 × 10^6 CFU/g), and sampling was conducted in the spring, summer, and fall of 1980–82, and during May 1983.

The study area was divided into six areas of uniform size. On each sampling date, a point that served as the center of a circular (7.62 m radius) sampling area was randomly-selected in each area. Locations for five 0.25 m^2 (0.5 × 0.5 m) quadrats were identified in each sampling area by randomly selecting compass headings and distances (30.48 cm intervals) along the selected compass headings. All waterhyacinth plants in each of 30 quadrats were removed and placed in a plastic bag until examination. All plants in each quadrat were examined for *Neochetina* (larvae and adults), *Sameodes* (larvae and pupae) and other arthropod species impacting the plant.

The first sampling trip was conducted immediately prior to application of the formulation. Waterhyacinth data (percent cover, biomass, density, height, and number of daughter plants) and plant pathogen data were obtained and compared in the same manner as data for the Assumption Parish site. Means for *Neochetina* adults and larvae/m^2 and *Sameodes* larvae and pupae/m^2 were calculated for each sampling date. Mean numbers of *Neochetina* adults and larvae/m^2 were weighted by plant density. ANOVA was used to determine whether calculated means varied significantly among sampling dates.

Results and Discussion

Assumption Parish

Mean values of waterhyacinth parameters measured at this site are shown in Table 1. The percent of surface area covered by waterhyacinth decreased from an average of 89.9% in May 1980 to 33.6% in July and 10.2% in September. Plant density decreased significantly from a mean of 116.7/m^2 in May to 40.5/m^2 in September. When weighted by percent cover, mean plant density declined from 104.8 plants/m^2 in May to 4.1 plants/m^2 in September. Although plant biomass declined in a similar manner, the differences were not significant. When weighted by percent cover, mean biomass declined from 10.6 kg/m^2 in May to 0.6 kg/m^2 in September. Mean plant height increased significantly from 8.0 cm in May to 22.2 cm in July, and showed a non-significant increase to 24.6 cm in September. Daughter plant production declined significantly from a mean of 31.3 plants/m^2 in May to 7.2 plants/m^2 in July.

Table 1. Means for waterhyacinth paramaters monitored during the *Cercospora* field application rate study.

Parameter	April 1980	July 1980	September 1980
Percent cover (%)	89.9	33.6	10.2
Plant density (No./m^2)	116.7 (±8.65)[1]	74.8 (±8.78)	40.5 (±7.59)
Plant density-weighted (No./m^2 * % cover)	104.8	25.2	4.1
Biomass (kg/m^2)	11.8 (±6.36)	6.1 (±1.38)	5.6 (±0.78)
Biomass-weighted (kg/m^2 * % cover)	10.6	2.1	0.6
Plant height (cm)	8.0 (±0.62)	22.2 (±3.03)	24.6 (±4.84)
Daughter plants (No./m^2)	31.3 (±6.04)	7.2 (±2.62)	6.5 (±3.79)

[1] Numbers in parentheses represent two standard errors of means.

Mean pathogen damage/leaf for all treatments, including untreated controls, are presented in Table 2. Mean values for all plots treated with *Cercospora* declined in July as compared to pretreatment values (May), but mean value for untreated controls increased slightly. Pathogen damage increased in all treated plots in September, but too few plants remained in the untreated control plots to allow sampling. Increased pathogen damage in September was not attributable to *Cercospora* because the fungus could only rarely be isolated from samples.

The mean number of *Neochetina* adults increased from 39.4/m^2 in May 1980 to 50.0/m^2 in July 1980, but significantly declined to 28.3/m^2 in September 1980 (Fig. 1). The mean number of *Neochetina* larvae increased from 54.5/m^2 in May 1980 to 97.6/m^2 in July, and then declined to 73.2/m^2 in September 1980 (Fig. 1); the mean numbers of both adults and larvae/plant were higher in September than in May due to the presence of fewer waterhyacinth plants in September.

Lake Theriot

Mean values of waterhyacinth parameters measured at this site are shown in Table 3. Percent cover of this study area by waterhyacinth remained at 100% throughout the 1980 and 1981 growing seasons. Percent cover by waterhyacinth declined from 80% in spring 1982 to 55% in fall 1982. Numerous other plant species were beginning to establish in the site by October 1982. However, a break in the floating barrier during winter 1982, allowed waterhyacinth from the adjacent marsh to re-invade the study site, and percent cover of the site by waterhyacinth was 90% in May 1983. Mean plant densities decreased throughout the growing season of each sampling year. Values were higher in spring 1980 (201.0/m^2) than in the spring of subsequent years. However, higher daughter plant densities in spring 1981 through 1983 suggested that the waterhyacinth population at the site was not as far along in seasonal development as was the waterhyacinth population in May 1980. It is speculated that plant densities would have been similar among the different years if the spring surveys had been conducted at more similar times of the growing season. However, because percent cover of waterhyacinth in the study area decreased significantly during 1982, weighted plant density values (number of plants/unit area in relation to the entire study site) showed that the waterhyacinth population decreased in number during the 1982 growing season (Table 3). Mean weighted plant densities were 31, 47, and 61% lower in April, July, and October 1982 samples, respectively, than in samples taken at comparable times in 1981. Mean biomass values showed the typical pattern of maximum biomass production during late summer months before a reduction in the fall. However biomass values showed a continual decline in waterhyacinth production in comparisons made between similar sampling dates of consecutive years. Peak biomass at the site was 30.4 kg/m^2 in 1980, 13.2 kg/m^2 in 1981, and 9.0 kg/m^2 in 1982. Furthermore, by weighting biomass values by percent cover estimates, it was shown that peak biomass in 1982 (July) was 79% lower than that of 1980 (July). Mean plant heights showed a similar decline throughout this study.

Table 2. Means of pathogen damage/leaf during *Cercospora* field application rate study. Means were calculated from three replicates of each treatment rate except where indicated.

Treatment rate[1]	April 1980	July 1980	September 1980
10^4	3.26	2.92*	7.71 +
10^5	3.22	2.89	6.95
10^6	3.15	3.06	7.35
C	3.42	3.60	-†

[1] Treatment rates expressed as number of colony forming units (CFU)/m^2.

* Based on two replicate plots.

+ Based on one replicate plot.

†Too few plants remained to allow sampling.

Mean pathogen damage (Fig. 2) decreased slightly during early summer of 1980 and then increased significantly during late summer and fall. Means of pathogen damage during subsequent years showed a progressive increase throughout each growing season,

Table 3. Plot means for waterhyacinth parameters monitored at the Lake Theriot study area.

Parameter	May 1980	Jul. 1980	Oct. 1980	Apr. 1981	Jul. 1981	Sept. 1981	Apr. 1982	Jul. 1982	Oct. 1982	May 1983
Percent cover (%)	100.0	100.0	100.0	100.0	100.0	100.0	80.0	70.0	55.0	90.0
Plant density (No./m^2)	201.0 (±16.06)[1]	100.7 (±6.97)	53.7 (±5.80)	110.7 (±10.53)	110.7 (±9.12)	66.3 (±5.23)	95.2 (±12.21)	83.1 (±7.69)	46.9 (±5.30)	93.5 (±8.07)
Plant density-weighted (No./m^2 • % cover)	201.0	100.7	53.7	110.7	110.7	66.3	76.2	58.2	25.8	84.2
Biomass (kg/m^2)	19.5 (±1.36)	30.4 (±1.60)	19.2 (±1.64)	5.7 (±0.63)	12.8 (±1.27)	13.2 (±1.13)	5.0 (±0.49)	9.0 (±0.97)	8.9 (±1.24)	11.5 (±0.85)
Plant biomass-weighted (kg/m^2 • % cover)	19.5	30.4	19.2	5.7	12.8	13.2	4.0	6.3	4.9	10.4
Plant height (cm)	31.2 (±1.94)	70.6 (±9.84)	77.1 (±3.27)	16.8 (±0.99)	39.2 (±2.34)	52.9 (±3.23)	11.3 (±0.84)	34.1 (±2.56)	42.5 (±3.76)	36.5 (±)
Daughter plants (No/m^2)	17.6 (±4.76)	0.8 (±0.71)	3.5 (±2.32)	32.8 (±8.14)	6.5 (±2.25)	2.1 (±0.92)	29.3 (±5.06)	3.9 (±2.12)	4.0 (±1.87)	28.3 (±5.85)

[1] Numbers in parentheses represent two standard errors of means.

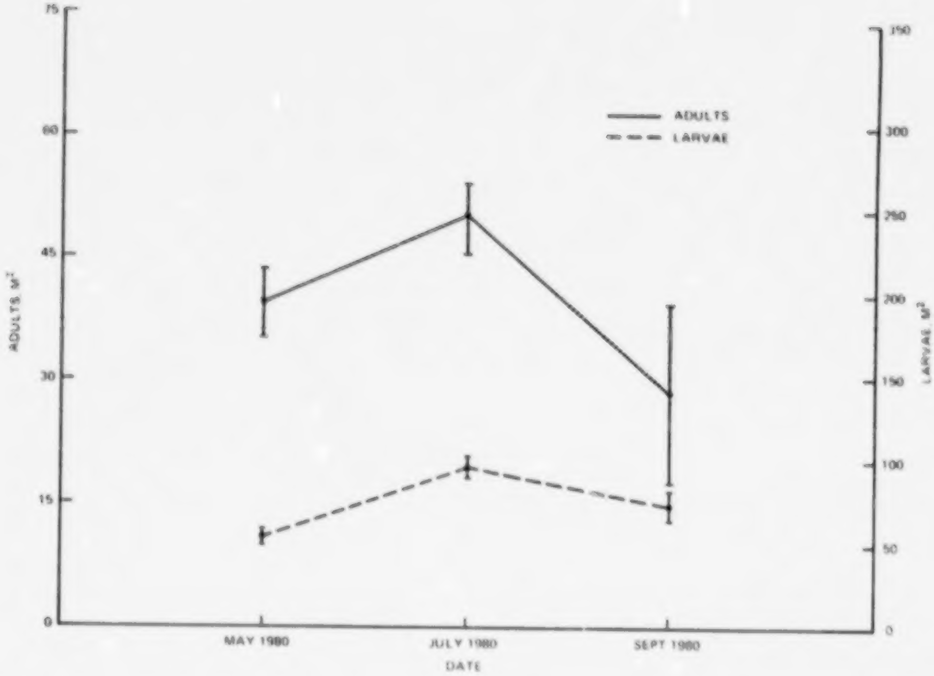

Fig. 1. Mean numbers of *Neochetina* adults and larvae/m² at Assumption Parish site. Vertical bars represent 2 SD of the means.

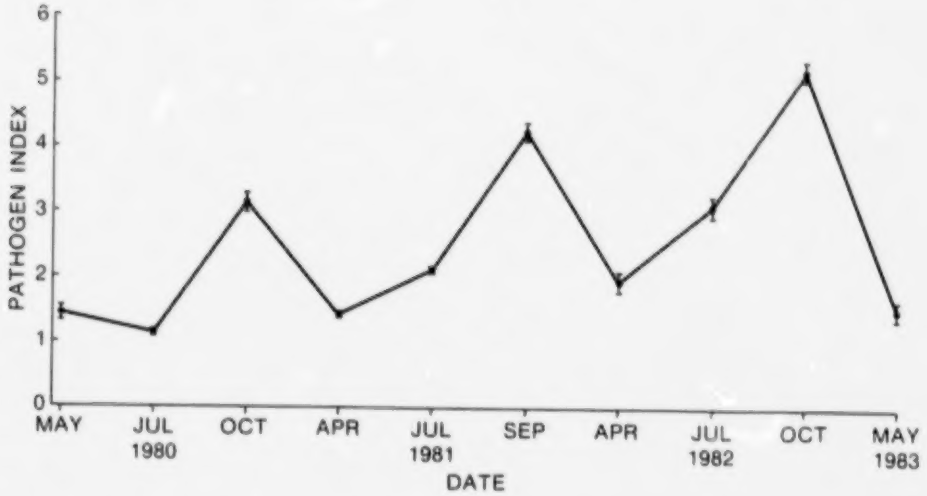

Fig. 2. Mean pathogen index values/leaf for the Lake Theriot site. Vertical bars represent 2 SD of the means.

and values for each sampling period through October 1982 were significantly higher than values from the same period of the previous year (Fig. 2). *Cercospora* was re-isolated from waterhyacinth tissues on all post-treatment dates prior to May 1982. Pathogen damage continued to increase in 1982, even though *Cercospora* could not be re-isolated from plant tissues after September 1981.

Mean numbers of *Neochetina* adults and larvae collected at the Lake Theriot site during this study are shown in Fig. 3. Numbers of adult weevils increased throughout the growing season during 1980, but obtained levels of only 6.7 adults/m^2 by October. The maximum number of larvae collected during 1980 was 44.8 larvae/m^2, also in October. Mean numbers of both adults and larvae were significantly higher in April 1981, with mean values reaching 11.7 adults/m^2 and 257.9 larvae/m^2. The *Neochetina* population continued to increase throughout early- to mid-summer. By July, the mean number of adults was 61.9/m^2. Larvae also showed a significant, but less dramatic increase to 312.8/m^2. Numbers of adults and larvae had decreased by September 1981, to 24.8 and 83.2/m^2, respectively, and numbers of *Neochetina* never again attained levels as high as during the first portion of the 1981 growing season. Numbers of *Neochetina* larvae remained at the September 1981 level into summer 1982, but decreased significantly to 50.0 larvae/m^2 by October 1982. Density of *Neochetina* adults increased throughout the 1982 growing season, attaining a seasonal maximum of 26.4 adults/m^2 in October. Numbers of adults declined to 10.4 adults/m^2 by May 1983.

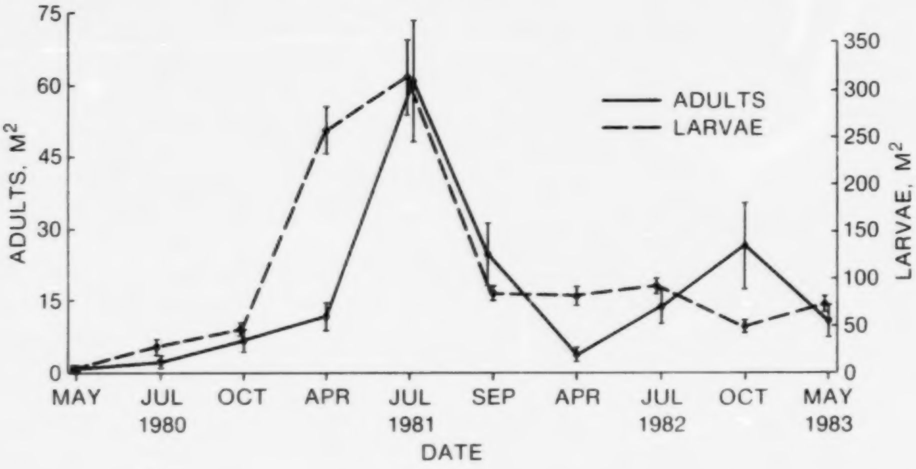

Fig. 3. Mean numbers of *Neochetina* adults and larvae/m^2 at the Lake Theriot site. Vertical bars represent 2 SD of the means.

Other arthropod species did not attain levels sufficient to significantly damage the waterhyacinth population. *Sameodes* was never collected in any samples, nor was evidence of its presence ever found during the study.

Waterhyacinth populations at both sites showed a significant reduction in production during the study. Reductions occurred during different years for each site and appeared to be linked to the establishment and development of the *Neochetina* population. When data collection began, a well-established *Neochetina* population was found at the Assumption Parish site, while the *Neochetina* population at the Lake Theriot site was not yet well-established.

Although data for only one growing season were taken at the Assumption Parish site before the waterhyacinth mat dropped out, significant reductions in percent cover, plant density, and number of daughter plants were recorded. Plant height increased from May to September (1980); however, the increase was only to a height of 24 cm, which is much smaller than the average height recorded at the other study sites (Sanders *et al.*, *in press*). This size reduction demonstrates the reduced fitness of the waterhyacinth population and indicates that the plants were stressed prior to the start of data collection. The *Neochetina* population present at the site in 1980 was not significantly larger than the *Neochetina* populations in healthy waterhyacinth infestations; however, our observations indicate that the weevil population was capable of destroying both the meristematic and photosynthetic portions of most plants. Because *Cercospora* was only rarely re-isolated from waterhyacinth tissues from the site, the role of this pathogen was considered non-significant in effecting the observed reduction. This view is emphasized because the high pathogen value at the site (Table 2) may otherwise unjustly implicate the role of *Cercospora*. The pathogen damage index values, as assessed in this study, represented a cumulative impact of all microorganisms. During fall months, these values were always high at all study sites, due to the deteriorating condition associated with normal senescence (Sanders *et al.*, *in press*). At the Assumption Parish site, pathogen damage values were high throughout the year because of an otherwise severely stressed waterhyacinth population, and not because of significant *Cercospora* infectivity.

Obviously, some factor had stressed the waterhyacinth at the Assumption Parish site prior to our study initiation in May 1980. Comparison between this site in 1980 and the Lake Theriot site in 1982 reveal certain similarities. At these times, both sites had waterhyacinth populations that were below normal in plant height, biomass, and density. Also, other aquatic plant species were beginning to compete with waterhyacinth for surface area dominance at both sites. Although one can only speculate as to the reason for the prior reduction in fitness of the waterhyacinth population at Assumption Parish, the Lake Theriot site offers evidence that a large *Neochetina* population during the first part of the growing season can inflict such a reduction.

The waterhyacinth population declined in percent cover, biomass, density, and plant height at the Lake Theriot site after the spring and summer peak in the *Neochetina* population. The weevil population expanded significantly in April 1981 and maintained relatively high levels. Examining the relationship of the number of *Neochetina* individuals (both larvae and adults)/kg plant tissue, we found that insect values were extremely high in April 1981 (49 individuals/kg) and July (32 individuals/kg). This four- to five-month sustained impact was apparently sufficient to reduce the ability of waterhyacinth to store food and produce new growth.

Goyer and Stark (1984) conducted a *N. eichhorniae* study during 1979 and 1980 at sites near Whitehall and Morgan City. Their findings were very similar to our results from the Assumption Parish and Lake Theriot sites. They found a reduction in percent cover, biomass, density, daughter plant production, and height and waterhyacinths were completely absent from the bayou at Morgan City, Louisiana by 1981.

The Louisiana Department of Wildlife and Fisheries estimates the waterhyacinth acreage in Louisiana annually at the end of each growing season. Fig. 4 depicts the estimated waterhyacinth acreage from 1974 through 1983 and some general trends can be observed. The acreage of waterhyacinth remained high through 1978, while the insect population was developing. A slight reduction in waterhyacinth acreage was observed in 1979. A swarming of *Neochetina* occurred in the south-central portion of the State adjacent to the Atchafalaya Basin in August 1980. The waterhyacinth population decreased drastically in 1980 to a level of 121,946 ha (301,100 acres). This represented a 75% reduction in waterhyacinth acreage from the 1974–78 average of 1.25 million acres. The waterhyacinth acreage gradually increased to a level of 243,000 ha (600,000 acres) in 1983, which was still 50% lower than the 1974-78 average.

Although the impact of *Neochetina* on the waterhyacinth population is significant, environmental factors assist and enhance the impact of the insects. During and prior to the establishment of *Neochetina*, environmental factors (e.g. extreme cold) occasionally reduced the waterhyacinth acreage; however, the growth capability of waterhyacinth was such that, after one growing season, the waterhyacinth acreage was again near or at its maximum.

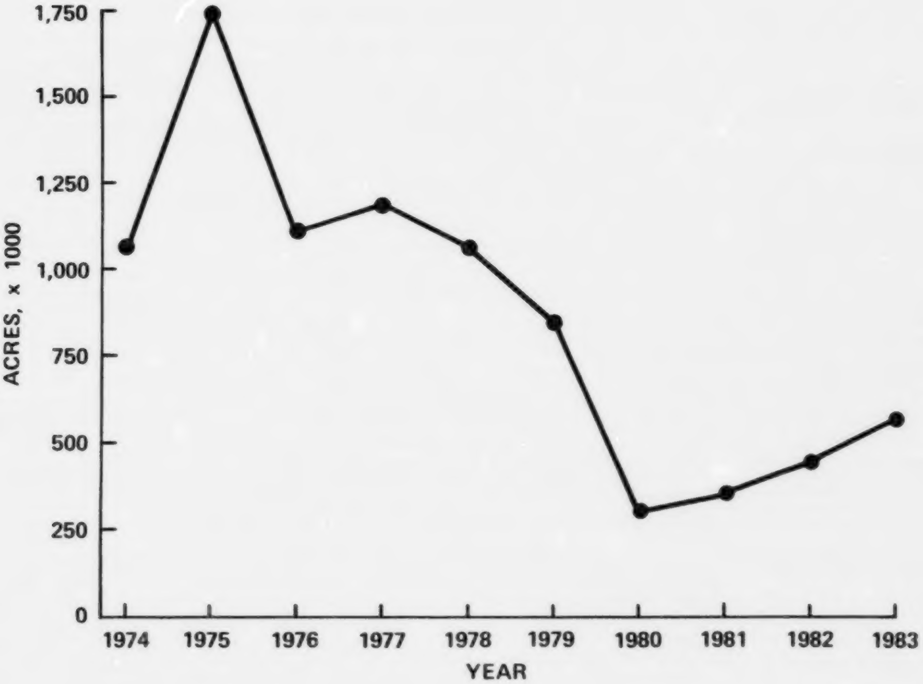

Fig. 4. Total acreages of waterhyacinth in Louisiana during 1974–83. Data provided courtesy of the Louisiana Department of Wildlife and Fisheries.

When *Neochetina* population levels become large enough to impact the plants, they reduce the ability of waterhyacinth to store food or produce growth. This impact also makes the plants more susceptible to environmental stress. Plants subjected to environmental stress do not recover in one growing season when impacted by large insect populations.

The increase in waterhyacinth acreage for 1981 through 1983 is predictable since *Neochetina* is host-specific to waterhyacinth and a reduction in waterhyacinth, the food source of *Neochetina*, effects a reduction in the *Neochetina* population. We predict that an oscillating pattern will occur in the waterhyacinth acreage in Louisiana, but the eventual amplitude of the oscillations remains a question.

Acknowledgments

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The Present Status of Grass Carp (*Ctenopharyngodon idella*) for the Control of Aquatic Weeds in England and Wales

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Abstract

The use of the herbivorous fish, the Chinese grass carp (*Ctenopharyngodon idella*), for water weed control in the U.K. has been studied experimentally for nearly 20 yrs. Now that they are fairly well understood, many grass carp are being released under license into private lakes, fisheries and drainage channels where weed management is essential. Detailed trials are still going on, however, with many data being collected. This paper attempts to summarise these and to describe the procedure involved before releases are allowed into waters, all of which come under Water Authority jurisdiction.

Utilisation Actuelle des Carpes Herbivores (*Ctenopharyngodon idella*) dans la Lutte Contre les Plantes Nuisibles Aquatiques au Royaume-Uni

L'utilisation de la carpe herbivore chinoise dans la lutte contre les plantes nuisibles aquatiques au Royaume-Uni a fait l'objet d'études expérimentales depuis environ 1968. Maintenant que les effets de ces poissons sont relativement bien connus, on ensemence actuellement dans lacs et des zones de pêche privées, sous réserve d'un permis. Toutefois, des essais détaillés se poursuivent et de nombreuses données sont rassemblées comme c'est le cas à l'Université de Liverpool. Le présent rapport vise à résumer ces essais et d'autres travaux ainsi qu'à décrire les politiques des diverses autorités en matière d'eau au sujet de l'ensemencement des carpes herbivores dans les eaux qui relèvent de leur juridiction. De façon générale, on croit que l'introduction de carpes herbivores est avantageuse, particulièrement si on utilise en même temps d'autres méthodes de lutte contre les plantes nuisibles.

Introduction

The grass carp (*Ctenopharyngodon idella* Val.; Cyprinidae) is a fish native to northe[illegible] China. It is almost completely herbivorous, being carnivorous for only the first fe[illegible] weeks of its life. Early publications (Hickling 1965; Pentelow and Stott 1965; Cross 1969) suggested that conditions in the U.K. might suit the use of this fish for controlling aquatic weeds. Very early experiments in England (Stott 1967; Stott *et al.* 1971; Stott and Robson 1970) showed that the fish could survive in our climate and that many of the more troublesome weeds were attractive to them.

Later, more detailed trials (Fowler and Robson 1978; Stott 1981; Buckley 1981; Fowler 1982, 1984; Moore and Spillett 1982; Mugridge *et al.* 1982) indicated no particularly adverse effects on indigenous or other introduced species of fish, or invertebrates, and confirmed that good weed control could be achieved. The danger, that once introduced, grass carp would breed naturally, was studied but the risk of their so doing is minimal as the fish need a simultaneous rapid rise in water flow and temperature, conditions not found in the U.K. Moore (1983), confirmed that grass carp are unlikely to affect freshwater environments more seriously than mechanical or chemical methods which are at present routinely employed.

The fish, however, were not always entirely successful in clearing the desired amount of weed. Most failures in Britain can be attributed to low water temperatures. The fish consume large amounts of weed only when water temperature is well above 16°C. Usually this only occurs in June, July and August by which time weed growth is well established. Recently we have experienced warmer springs than usual and the fish were able to graze the early weed growth before it got too thick. Even so, many water bodies may be too cold even in summer, because they are too deep, too shaded, or rely on cold spring water supplies (Mugridge *et al.* 1982).

Predation is another bar to grass carp success. A trial in a canal in the southeast of England was thought to have failed because of the presence of a large pike population (Dr. B.R. Buckley and Mr. K. Wilson, Southern Water Authority, pers. comm.). Also the fishes' preference for some plants (e.g. *Elodea canadensis* Michx., Hydrocharitaceae, and *Potamogeton pectinatus* L., Potamogetonaceae) over others (e.g. *Myriophyllum spicatum* L., Haloragaceae, *Ceratophyllum demersum* L., Ceratophyllaceae, and some algae) is critical and it must be ensured that the weed problem present is one with which the fish can deal.

Fish of a reasonable size (at least 100 g) seem to survive cold winters where there is some ice cover, although it is becoming apparent that in mild winters, where the water temperature remains in the region of 10°C, the fish are still reasonably active, but do not eat. This may be detrimental to their survival. Their weakened condition in February and March leaves the way open for parasites (i.e. flukes, *Gyrodactylus* sp. and *Dactylogyrus* spp.; the flagellate, *Costia* sp. and the ciliates *Chilodinella* and *Trichodina* spp.) (Dr. B.R. Buckley, pers. comm.). I have also noticed *Argulus foliaceus* and small leeches on 12–15 cm fish in February which resulted in deaths.

In spite of these limitations, the greater understanding of the needs of the fish has encouraged water authorities to initiate larger trials. Recently, some individuals and public corporations have also been licensed to stock fish in small enclosed waters.

Most grass carp introductions are aimed at reducing, not eliminating, weeds. Some plant life is essential to permit maintenance of a balanced aquatic ecosystem. Overgrazing by grass carp can encourage the predominance of inedible plant species including some species of filamentous algae (Fowler and Robson 1978; Fowler 1984).

Only in areas of low-lying, valuable arable land such as the Fens in Eastern England, much of which is below mean sea level and where an efficient drainage system is essential, is water weed in any quantity difficult to accept (Cave 1981). Even here there is conflict of water use and drainage engineers now accept that some weed is tolerable, providing the risk of flooding especially in the summer is minimised (Honnor 1984). In July 1968 an 8-hr storm resulted in floods which destroyed 24,000 ha of crops in the Welland and Nene area of the Fens (Miles 1976). Heavily weedy drainage channels prevented the flood water reaching the pumping stations.

Present Research and Development

Much of the research work on aquatic weed control is, at present, aimed at reducing costs as these mount up year by year. Chemicals become more expensive and the buying, maintenance and running costs of machinery increase. Grass carp could help reduce these costs. In the 4th District Main Drain, near Spalding in Lincolnshire (which is 3.2 km long and 5 m wide) the cost of a twice-yearly cut is currently £945. In summer

1983, 504 grass carp, average weight 330 g, were introduced. By August, grazing was evident on the beds of *Callitriche* sp. (Callitrichaceae). Although emergent and bank-side growth had to be cut in October and some *Vaucheria dichotoma* Ag. (after Walz) which is not touched by the fish was removed, the cost of the summer cut was saved. The evidence seen in 1984 is that the control is improving (Mr. J. Honnor, Welland and Deeping Internal Drainage Board, pers. comm.). Although the initial cost of the fish (£10/kg) is high, their survival is good and their influence will increase with their biomass and should last many years.

Biologists in the Wessex Water Authority are very interested in grass carp for weed control. An initial trial in an isolated ox-bow lake of the River Axe, showed that the fish could bring about a highly significant reduction in weed growth. Consequently, other sites have been stocked and a major drain is to be stocked in 1984. It is hoped that this will provide a convincing demonstration of the potential of grass carp to the Authority's land drainage engineers.

Thames Water Authority has allowed licensed introductions of grass carp, including some to flooded gravel pits. Many of these pits are used now for fishing, water skiing and sailing and the predominant weed is nearly always Canadian pond weed (*E. canadensis*). This is an introduced plant, first recorded in the British Isles in 1836 (Perring and Walters 1962) and usually infests newly made lakes. It is appropriate that by introducing another exotic species, the grass carp, we can perhaps control the problem.

Currently the most ambitious and detailed trial was started in 1982 by the University of Liverpool in part of the Lancaster Canal in northwest England (Dr. J. Eaton and colleagues, Liverpool University, pers. comm.). Fish-proof barriers were installed to enclose 0.2 ha areas, and two stocking densities of 200 and 100 kg/ha together with controls were replicated. Frequent assessments of weed growth, water quality and invertebrate fauna are being made and fish survival and growth are monitored.

As well as numerous submerged plant species, the canal supports a large amount of floating plants (mostly *Lemna minor* L.; Lemnaceae). The 100 kg/ha stocking density has reduced the submerged weed, but has had little impact on the floating weed. The higher stocking density significantly reduced both floating and submerged species, effecting about a 60% reduction in the peak summer crop of total weed in the first year, and about 75% reduction in the second year.

As part of this project, fish behaviour studies have been carried out using a radio-telemetric system. Five fish were tagged and released into a 1.2 km section of the canal already containing 70 or 80 grass carp. Preliminary findings suggest that the fish feed in loosely attached shoals, grazing for some time in one patch before individuals move off at speed, for no apparent reason, to another patch, where they resume eating. Only three distinct feeding areas appeared and although this type of grazing will not reduce the weed growth evenly there are certain advantages of an ecological nature. Patchy clearance increases the diversity of the channel environment by creating areas of open water within which free-swimming invertebrates proliferate. The open areas also experience more stable oxygenation than do thickly vegetated areas where plant photosynthesis and respiration commonly result in violent day/night cyclic variations in dissolved oxygen concentrations. Clear areas will obviously please fishermen.

The Yorkshire, Severn-Trent and Welsh Water Authorities all have small ponds and lakes stocked with grass carp and are taking great interest in the results. The 10 Water Authority areas and the approximate positions of all introductions are shown on Fig. 1.

Legislation

If a person or organisation wishes to put grass carp into their water, the local Water Authority must be satisfied that the proposed site is suitable and that grass carp would be successful. Under section 30 of the Salmon and Freshwater Fisheries Act (1975) fish cannot be released without Water Authority permission. This also applies to the movement of fish from one place to another. The Authority, if permission is given, also insists on some degree of reporting on the progress of the fish.

In order to further protect our environment the Wildlife and Countryside Act (1981) states that 'it is an offence to release *into the wild* any animal, including fish and shellfish, which is not normally resident in, or a regular visitor to Great Britain *in the wild*'. The exact interpretation of what is meant by '*in the wild*' is open to debate, but there must certainly be no possibility of the fish escaping into a river system.

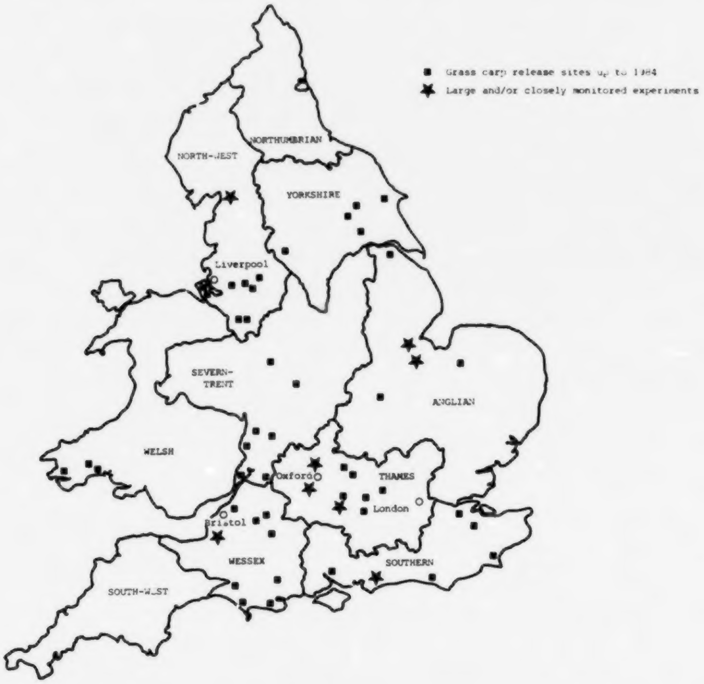
■ Grass carp release sites up to 1984
★ Large and/or closely monitored experiments
NORTHUMBRIAN
NORTH-WEST
YORKSHIRE
Liverpool
SEVERN-TRENT
ANGLIAN
WELSH
Oxford
THAMES
London
Bristol
WESSEX
SOUTHERN
SOUTH-WEST

Fig. 1. Map of England and Wales showing Water Authority boundaries and sites of grass carp introductions up to 1984.

The Grass Carp Field Trials Steering Committee (consisting of representatives from Water Authorities, Internal Drainage Boards, Universities, the Ministry of Agriculture, Fisheries and Food, the Nature Conservancy Council, The Weed Research Organization and the British Waterways Board) has been meeting annually to discuss experiments and policy. The committee has also produced a simple guide to would-be users, which gives essential information about the fish, their likely effects, the conditions and plants suitable and the procedure to be followed before applying for a license.

If all these bodies are satisfied then the Ministry of Agriculture will issue a license (for a fee of £20). In spite of all these somewhat daunting impediments a number of licenses have been issued to individuals, to fishing clubs and public bodies to stock private lakes, fisheries or park lakes (Table 1).

Availability

Grass carp are still not widely available and there is at present only one commercial source in Britain. Imported supplies are limited because of the inability of most foreign producers to meet our disease requirements. The Ministry of Agriculture, Fisheries and Food has bred grass carp successfully (Stott and Durbin 1980) and also some of the Water Authorities have their own breeding programmes, and have stockable-sized fish available. Southern Water Authority has been able to supply fry and fingerlings to sister organisations.

Table 1. Field trials and other grass carp introductions in the UK.

Date	No. of introductions	Organizations responsible[1]
Pre - 1971	4	MAFF and WRO
1977	4	WRO and WA
1979	5	WRO and WA
1980	2	WA
1981	12	WA
1982	7	WA
1983/4	29	WA, IDB and Private

[1]MAFF = Ministry of Agriculture Fisheries and Food.
WRO = Weed Research Organization.
WA = Water Authority.
IDB = Internal Drainage Board.

The actual production of eggs and fry is well understood, but the growing on of grass carp in large numbers to an appreciable size requires major facilities with warm water for all of the first year. Small numbers of fish are no problem, although rearing is time-consuming as the very young fish need live food before gradually progressing to vegetable feeds at about 6–8 wks old. Bringing on fry in outside ponds is being done, but the process is longer and more hazardous. Reading University together with Thames Water Authority has initiated trials on the best way of bringing fish up to a stockable size. They are employing glasshouses and polyethylene 'tunnels' erected over tanks and excavated ponds to provide the warmth necessary for fish growth (Domaniewski 1983). Wessex Water Authority is also artificially raising fry in warm water re-circulation systems, and has some experiments in lagoons under polyethylene 'tunnels'. Fry are also being grown on to stockable size (300–700 g) by a commercial cyprinid fish farm and some small lakes (0.5–1 ha) have been stocked experimentally with young fish (Mr. A. Frake, Wessex Water Authority, pers. comm.).

It could still be some years before reliable sources of disease-free appropriately sized grass carp are extensively available in the U.K.

There is now confidence about the future of grass carp in the U.K. It is accepted that they are not the answer to all weed problems, but they can complement other more established methods and, sometimes may be the only alternative to no weed control at all! There is a constant flow of enquiries from interested people but the scarcity of fish, the licensing procedure and the knowledge and experience of water authority scientists, who make the decisions on whether to allow grass carp to be introduced, should ensure that unnecessary releases do not occur.

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Universities: Dr. D.C. Hockin and Dr. J.W. Eaton, Dr. K. O'Hara and Dr. J.O. Young, Liverpool. Dr. J.C.J. Domaniewski, Reading.

Ministry of Agriculture, Fisheries and Food: Mr. B. Stott, Mr. I. Russell and Miss A. Henri.

Welland and Deeping Internal Drainage Board: Mr. J. Honnor.

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A Summary of Research into Biological Control of Salvinia in Australia

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Abstract

A weevil (*Cyrtobagous salviniae*) is controlling *Salvinia molesta* at an increasing number of sites in Australia, but a moth (*Samea multiplicalis*), though breeding and dispersing more rapidly than the weevil, is not. Temperature and availability of nitrogen are usually the most important factors controlling population growth rates of both the weed and the control agents. Experiments, field monitoring and modelling are being used to investigate how different conditions of climate and nutrition affect the dynamic equilibrium reached by the weed and insects. Prospects are good for being able to predict the effects of agents under different conditions in this comparatively simple system and, in the process, gain further insights into plant-herbivore dynamics.

Résumé des Recherches Relatives à la Lutte Biologique Contre *Salvinia molesta* en Australie

En Australie, le charançon *Cyrtobagous salviniae* est un agent de lutte biologique efficace contre *Salvinia molesta* dans un nombre croissant d'emplacements, contrairement au lépidoptère *Samea multiplicalis* bien qu'il se reproduise et se disperse plus rapidement que le charançon. La température et la présence d'azote sont habituellement les plus importants facteurs influant sur le taux de croissance des populations de *Salvinia* et d'agents biologiques. Au moyen d'essais, de surveillance sur le terrain et de modélisation, les chercheurs tentent de déterminer l'influence de divers paramètres climatiques et nutritifs sur l'équilibre dynamique des plantes nuisibles et des insectes. Cette méthode relativement simple semble offrir de bonnes possibilités pour la prévision des effets des agents biologiques dans diverses conditions et permettra également de rassembler d'autres données sur la dynamique plante-herbivore.

Introduction

Since the 1930s *Salvinia molesta* Mitchell (Salviniaceae) has been spread by man to Africa (Hattingh 1961; Gaudet 1976; Edwards and Thomas 1977), India (Cook and Gut 1971; Thomas 1979), Sri Lanka (Senaratna 1943; Chow *et al.* 1955), S.E. Asia (Arumugam and Furtado 1974; Soelastri and Tjitrosoepomo 1974), the Pacific (Johnstone 1969; Sundaresan and Reddy 1979; Mitchell *et al.* 1980) and Australia (Mitchell 1978). The weed is free-floating and causes problems by forming thick mats covering the surfaces of lakes, canals, paddy fields and slow-moving rivers.

S. molesta was recognised as being distinct from *S. auriculata* Aublet in 1972 (Mitchell 1972). Prior to this, attempts at biological control of *S. molesta* by the CIBC using insects collected from *S. auriculata* in Trinidad either failed or gave equivocal results (Bennett 1975; Kamath 1979; Mitchell and Rose 1979). CSIRO Australia started work on *S. molesta* in 1978 in South America and the previously unknown native range of the plant was discovered in S.E. Brazil (Forno and Harley 1979; Forno 1983). Three potentially useful insects were found and imported into quarantine in Australia: *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae); *Samea multiplicalis* (Guenée) (Lepidoptera: Pyralidae); and *Paulinia acuminata* (De Geer) (Orthoptera: Pauliniidae). After testing to ensure adequate host-specificity and freedom from their own natural enemies, *C. salviniae* and *S. multiplicalis* were released, but *P. acuminata* will not be released unless evaluation of the other two species suggest that it could improve the degree of control achieved.

Compared with other attempts at biological control of weeds, particularly those involving terrestrial weeds, the system containing *S. molesta* and its control agents in Australia is remarkably simple. The plant is a sterile pentaploid (Loyal and Grewal 1966) in which the entire species appears to be a single genet, it occupies a highly uniform two-dimensional habitat (the water surface), it suffers no water stress, in many waterbodies there are no other plants competing with it for space, and it is not attacked significantly by any natural enemies other than the introduced control agents. In addition, study of the system is comparatively easy because all parts of the plant are accessible without excavation and because the high rate of growth in good conditions allows experiments to be carried out quickly. It was recognised that this situation offered a unique opportunity to make a complete system study at minimal cost and it was decided to attempt to measure all of the most important interactions which ultimately determine the degree of control achieved.

Fig. 1 presents a conceptual model of what are thought to be the most important interactions and it is being used as a framework for integrating individual studies. It is hoped this approach will give some insight into such practical questions as what determines whether a given control agent will be effective or ineffective, whether different agents acting together are synergistic or interfere, and how the environment and insect damage interact to determine plant productivity. As Crawley (1983) has pointed out, there does not appear to be a single system for which the main determinants of abundance have been elucidated for both a plant and its herbivores and theory will continue to outstrip empirical understanding to an embarrassing extent until a body of such studies is accumulated.

Components of the Research Programme

Studies of the Plant

Temperature was expected to be an important variable affecting both plant and insects and it was suspected that temperature records from weather stations, which could be used in predicting the outcome of biological control in different climates, would differ from temperatures actually experienced by *S. molesta*. Consequently, a study was conducted to allow temperatures experienced by the plant to be predicted from standard meteorological data. It was found for one site that the plant was warmer than the air in a nearby Stevenson's screen most of the time and that good predictions of hourly temperatures experienced by the plant could be made from daily air maximum and minimum temperatures and a term representing inertia in seasonal changes of water temperature (Room and Kerr 1983). The generality of these findings has yet to be validated for other sites.

The studies of effects of temperature and nutrients on growth by *S. molesta* by Mitchell and Tur (1975) and Cary and Weerts (1981) are being extended, particularly in the field. It has been found that growth rate can be predicted with some accuracy using corrected weather station temperatures and the concentration of nitrogen in the plant. Flushes of nutrients in water, as occur in runoff after heavy rain, resulted in peaks of nitrogen and phosphorus concentrations in plant tissues several days later, followed by peaks in growth rate after another week. The critical concentration of nitrogen in plant tissues for growth was found to be near 0.9% dry weight and there was a rapid drop in tissue concentrations of nitrogen and phosphorus as buds developed into mature ramets.

Being sterile, population growth in *S. molesta* is entirely dependent on survival and development of meristems. Studies have been made of the spatial arrangement and dynamics of meristems (Room 1983) and computer models have been built to simulate population change under different conditions of insect and nutrient supply (Room 1985).

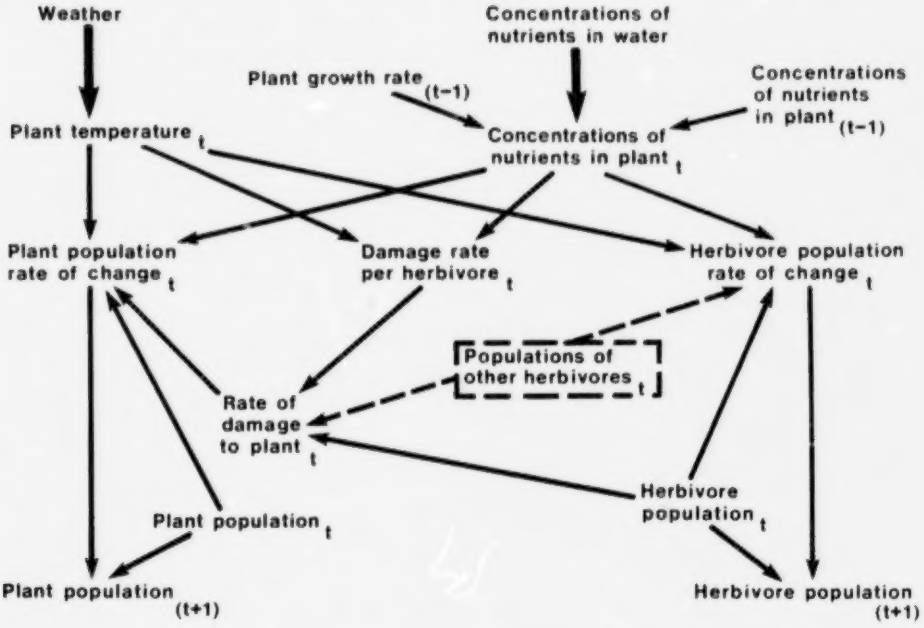
Weather
Concentrations of nutrients in water
Plant growth rate (t−1)
Concentrations of nutrients in plant (t−1)
Plant temperature t
Concentrations of nutrients in plant t
Plant population rate of change t
Damage rate per herbivore t
Herbivore population rate of change t
Populations of other herbivores t
Rate of damage to plant t
Plant population t
Herbivore population t
Plant population (t+1)
Herbivore population (t+1)

Fig. 1. Conceptual model of the most important interactions expected to take place between *Salvinia molesta* Mitchell and a biological control agent. This model is used to plan and integrate studies of particular interactions. Arrows go from independent to dependent variables and complexities due to the presence of a second control agent are indicated by dashed lines. t = time interval.

The models showed, for example, that growth of a typical population of the weed should be stopped by destruction of 50% of all buds which start to develop. Experiments are underway to examine the effects of insect damage and manual clipping on plant growth. Field experiments investigating the relationships between temperature, nutrients, insect damage and plant growth have shown a range of effects from reduced plant growth, to compensation, and even stimulated growth.

Laboratory Studies of Cyrtobagous salviniae

It was initially thought that the *Cyrtobagous* sp. found on *S. molesta* in Brazil was *C. singularis* (Forno 1981; Forno *et al.* 1983) and it was hoped that a biotype had been obtained which would be more effective against *S. molesta* than that collected from *S. auriculata* in Trinidad by Bennett (1975). However, comparison of the morphology and biology of insects from the two sources showed that those from *S. molesta* were a different, then undescribed species of *Cyrtobagous* (Sands 1983; Sands and Schotz 1985). The new species was subsequently named *C. salviniae* (Calder and Sands 1985).

The biology of *C. salviniae* was described by Forno *et al.* (1983) and Sands *et al.* (1983). The insect can only breed on species in the genus *Salvinia* (Forno and Bourne 1984). In laboratory tests adults fed actively on *Pistia stratiotes* L. (Araceae) and produced a single feeding scar on *Ipomoea batatas* (L.) Lam. (Convolvulaceae), but no breeding took place and none of a further 44 plant species was attacked. Laboratory studies have suggested minimum temperatures for various activities as follows: oviposition 21°C; egg hatch 19°C; larval development 16.3°C; pupal development 19.6°C; adult feeding 13°C; and have determined the effects of different constant temperatures on rates of development. The optimum temperature was 30°C, at which the complete life-cycle occupied 6 wks. An increase of 0.5% in the dry weight concentration of nitrogen in *S. molesta* decreased larval development time by 4.1 days at all temperatures and more than doubled the fecundity of adult females (Sands and Schotz, pers. comm.). Adults preferentially attacked buds, known to contain more nitrogen than other tissues, but varying the concentration of nitrogen had no effect on feeding activity.

Adult *C. salviniae* each destroyed about five buds of *S. molesta*/wk and live for 8 wks at 26°C. During their development, larvae each tunnelled through 2.4 sections of rhizome containing < 1.5% N or 1.2 sections containing > 1.5% N. Feeding by adults alone and by larvae alone has been observed to reduce growth by *S. molesta* significantly and experiments are in progress to relate the effects on growth to population densities of the insect, temperatures and availability of nitrogen.

Laboratory Studies of Samea multiplicalis

Information on the biology of *S. multiplicalis* additional to that recorded by Bennett (1966), Sankaran and Ramaseshiah (1973), Knopf and Habek (1976) and DeLoach *et al.* (1979) has been presented by Sands and Kassulke (1984) and Forno and Bourne (1984). In addition to *Salvinia* spp. the species breeds on *P. stratiotes* and *Azolla pinnata* R. Br. (Salviniaceae). It produced feeding scars on 13 of a further 50 species of plants, none of which supported complete larval development. Prior to release in Australia, much effort was expended in eliminating a *Nosema* microsporidian disease from the colony imported from Brazil.

Experiments in progress suggest that the optimum temperature for development is close to 30°C, at which the life-cycle takes about 24 days to complete. The minimum temperature for development is close to 11°C and all larvae held at constant 36°C died. Taylor (1984) showed that larvae fed *S. molesta* containing < 1.35% nitrogen in their first two instars pass through a supernumerary moult and spent up to 70% more time developing to pupation. In addition, larval mortality was higher when larvae were fed low-nitrogen tissues, and adult females which developed from larvae fed on plant tissues containing 2% nitrogen matured twice as many eggs as females from larvae fed on tissues containing 1% nitrogen.

Larvae of *S. multiplicalis* chew holes through the expanded leaves of *S. molesta*, consuming the equivalent of four mature leaves during development. Experiments are in progress to measure the effects of this damage on growth by the plant. Initial results indicate that the plant can sustain very high levels of leaf destruction without losing the ability to regrow.

Field Monitoring of Releases

The first release of *C. salviniae* was spectacularly successful, with the insect destroying the largest infestation of *S. molesta* in Australia, of some 10,000 tonnes, in less than 1 yr (Room *et al.* 1981). This insect has become established at sites from Brisbane to Cairns along the east coast, at Darwin and Mt. Isa (Room *et al.* 1984) and in Papua New Guinea (Thomas and Room 1985). Air temperatures at these sites have ranged from < 0°C to > 45°C and the weed has been, or appears to be in the process of being controlled at all of them. In all cases, *C. salviniae* has dispersed initially at rates of only a few metres/month. Berlese funnels have been found to give accurate estimates of adult population densities (Boland and Room 1983).

S. multiplicalis has been released, and become established at several sites in north-eastern Australia and spread at least 170 km north and south in 20 months (Room *et al.* 1984). Air temperatures at the sites colonised ranged from < 0°C to > 45°C. Populations of the insect have repeatedly caused extensive damage to *S. molesta* but the weed has regrown following decline in the insect populations and is not considered to be under control. Population crashes of the insect have coincided with periods of high temperature and native Australian parasites have been reared from field-collected larvae.

An experiment is in progress in which *C. salviniae* and *S. multiplicalis* are being released separately, into two cages each, at each of three sites separated by 600 km on a north–south transect. The *S. molesta* in one of each pair of cages is being fertilised with urea and it is hoped to gain useful information on the effects of climate and nutrition on interactions between the plant and its herbivores. The results to date show that application of urea can greatly increase the rates of population increase of the plant and of both insects.

S. multiplicalis breeds faster and disperses faster than *C. salviniae* and it would be reasonable to expect the former to be the more effective control agent. At this stage there seem to be five possible explanations why this is not the case. Compared with *C. salviniae*: (1) *S. multiplicalis* causes damage which has less effect/unit of tissue removed; (2) it suffers mortality from native Australian parasites; (3) it is more sensitive to high temperatures; (4) intra-specific competition may stop population densities from being maintained at levels sufficient to destroy the ability of the plant to regrow; and (5) it may be more susceptible to damage-induced defences (Rhoades 1983) produced by the plant. These effects are not necessarily mutually exclusive and may not apply to the same extent once *S. multiplicalis* becomes established in cooler, more southerly parts of Australia.

The Future

Populations of the plant and insects in the field will continue to be monitored to observe the dynamic equilibria and geographical limits attained and to evaluate possible effects of native Australian predators, parasites and pathogens on the insects.

Feeding by *C. salviniae* which damages buds and rhizomes, and by *S. multiplicalis*, which damages leaves, is likely to have different effects on the quality of undamaged tissues remaining, and experiments are planned to investigate this and other aspects of interference or synergism between the two insects. The results, and those of the other studies described above, will be used to extend the models of plant growth to include insect dynamics and their effects. A model of the plant–herbivore system, driven by weather and nutrients, will then be used to make predictions about the geographical limits of the component species and the degree of control to be expected in contrasting environments. It is hoped to test the model, and the understanding of the system that it represents, by creating new, isolated, infestations of *S. molesta* in different parts of Australia and then releasing the insects on them.

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Control or No Control: A Comparison of the Feeding Strategies of Two Salvinia Weevils

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Abstract

The feeding behaviour of two *Cyrtobagous* spp. can be used to explain their different potential as biological control agents of salvinia (*Salvinia molesta*). In laboratory experiments, adults of *Cyrtobagous salviniae* fed mainly on buds whereas *C. singularis* fed extensively on other parts of the plant, leaving more buds intact. Larvae of *C. salviniae* tunnelled into rhizomes, destroying the vascular bundles; larvae of *C. singularis* mainly fed externally on buds and other exposed tissues of the plants. The greater effect of *C. salviniae* on salvinia by destroying rhizomes and more buds, may explain its success as a biological control agent of salvinia where *C. singularis* had previously failed.

Efficacité des Agents Biologiques: Comparaison des Stratégies d'Alimentation de Deux Charançons de Salvinia

Deux *Cyrtobagous* spp. ont un potentiel différent comme agents de lutte biologique contre la plante nuisible *Salvinia molesta* en raison de leurs habitudes alimentaires distinctes. Les adultes de *Cyrtobagous salviniae* se nourrissent principalement de bourgeons, tandis que *C. singularis* s'alimente principalement d'autres parties de la plante, détruisant ainsi moins de bourgeons. Les larves de *C. salviniae* pénètrent dans les rhizomes, où ils détruisent le faisceau libéro-ligneux, tandis que les larves de *C. singularis* mangent principalement des bourgeons et d'autres tissus exposés des plantes. *C. salviniae* est sans doute un agent biologique plus efficace dans la lutte contre salvinia que *C. singularis* parce qu'il détruit les rhizomes et de plus grandes quantités de bourgeons.

Introduction

When biological control of the water weed salvinia (*Salvinia molesta* D.S. Mitchell; Salviniaceae) was achieved in Australia, the success was attributed to introduction of a biotype of *Cyrtobagous singularis* Hustache (Coleoptera: Curculionidae), which was specially adapted to *S. molesta* (Room *et al.* 1981; Forno *et al.* 1983). Failure to control the weed in several other countries (Julien 1982) was thought to be due to introduction of a biotype collected from a different plant species, *S. auriculata* Aublet.

Studies were carried out on weevils originating from Trinidad (collected from *S. auriculata*) and Brazil (collected from *S. molesta*) to determine if the existence of the biotypes could be identified experimentally. Morphological studies of the two populations subsequently confirmed that they were different species (Sands 1983). The weevil introduced into Australia for biological control of *S. molesta* was not *C. singularis*, but represented the closely-related species *C. salviniae* Calder & Sands (Calder and Sands 1985).

Feeding by larvae of *C. salviniae* was investigated by Sands *et al.* (1983) who reported that the destruction of salvinia was primarily due to tunnelling by larvae within the rhizomes. In this paper we describe a series of experiments in which we compared the feeding characteristics of the two *Cyrtobagous* spp. and discuss their potential as biological control agents for *S. molesta*.

Materials and Methods

The Salvinia Plant

Salvinia plants are free-floating ferns. Their submerged rhizomes consist of nodes interconnected by internodes, each node bearing two floating leaves and a submerged, modified leaf referred to as a root, a leaf bud at the apical growing point, and buds at the base of leaves where branching commences.

The histology of the salvinia stem (the rhizome) was shown by Croxdale (1981) to be similar to that of the leaf petiole. In cross section the salvinia rhizome contains a central core of vascular bundles or protostele, surrounded first by an endodermis, then a spongy, air-filled aerenchyma which in turn is surrounded by a thin-walled layer of epidermal cells. The protostele branches at nodes, entering the leaf and root petioles and branches again as it enters the lamina of the leaf or the branches of root.

Experiments with Weevils

Experiments with *C. salviniae* collected from Mt. Isa, Queensland, but originating from Joinville, Brazil (on *S. molesta*), and *C. singularis* from Manzanilla, Trinidad (on *S. auriculata*), were carried out in a quarantine insectary using the culture methods described by Forno *et al.* (1983). All experiments were carried out on *S. molesta* after it was confirmed that *C. singularis* had similar feeding characteristics on its native host, *S. auriculata* (unpubl. data). Comparative studies of both *Cyrtobagous* spp. were made at 25°C in controlled-temperature cabinets. The insects were provided with secondary- or tertiary-stage plants of *S. molesta* grown in a nutrient solution containing 3.0 mg/l equivalent of nitrogen (as in Sands *et al.* 1983). To compare feeding by larvae, 10 newly-emerged larvae of each species were placed within an apical bud of a rhizome of *S. molesta* using the method described by Sands *et al.* (1983). Observations and measurements were made every 3 days until pupation took place.

In experiments with adults, 10 females of each weevil species were provided with four rhizomes of *S. molesta* which were replaced every 3 days. The numbers of primordial buds (buds beginning to swell) totally destroyed were compared since advanced buds usually continued to develop following attack (unpubl. data). Observations and measurements were made every 3 days for 15 days.

Results and Discussion

Larval Damage

Larvae of both *Cyrtobagous* spp. after hatching, begin to feed on roots and buds of salvinia. Within a few days larvae of *C. salviniae* begin to tunnel into the rhizomes where they progressively destroy the nodes, internodes and sometimes damage the roots (Sands *et al.* 1983).

Damage resulting from tunnelling by larvae of *C. salviniae* varied according to stage and toughness of the salvinia plant. When feeding in primary- or secondary-stage plants (defined by Mitchell and Thomas 1972), larvae consumed the protostele, endoderm, meristems and much of the aerenchyma (Fig. 1A), but when tunnelling in tertiary-stage plants, feeding was confined mainly to the endoderm, meristems and aerenchyma, leaving some of the tough protostele intact (Fig. 1C). When larvae of *C. salviniae* tunnelled into nodes, adjoining leaves and internodes usually separated, turned brown and eventually disintegrated. Each larva is known to destroy from 1.2–2.4 rhizome sections (Sands *et al.* 1983), including nodes, from which regrowth could otherwise have taken place. In contrast, larvae of *C. singularis* did not tunnel within rhizomes but moved from one site to another, feeding mainly externally on the submerged parts of the plant, particularly on buds, rhizome aerenchyma, and leaf petioles (Fig. 1B, 1D).

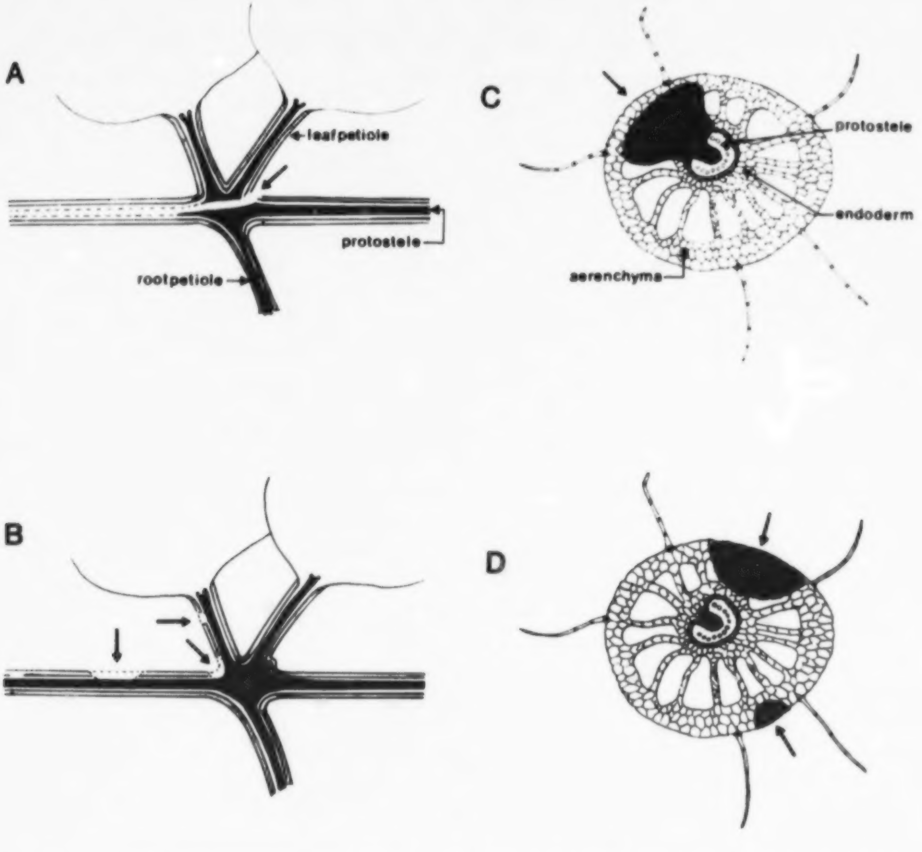

Fig. 1. Feeding sites of *Cyrtobagous* spp. larvae on *Salvinia molesta* D.S. Mitchell: (A, C) by *C. salviniae* Calder & Sands, (B, D) by *C. singularis* Hustache; (A, B) lateral view of rhizome, secondary stage; (C, D) transverse section of rhizome, tertiary stage.

In these experiments, each *C. salviniae* larva destroyed only one bud before tunnelling into the rhizome, but each larva of *C. singularis* destroyed an average of three buds and fed at many separate sites on the rhizome. While they sometimes tunnelled into the leaf petioles and fed on the aerenchyma of the rhizomes, larvae of *C. singularis* did not destroy the protostele in nodes of secondary-stage plants, nor the endoderm of tertiary-stage plants. Large larvae have never been observed totally encased in the rhizome, whereas this is the usual feeding site for similar stages of *C. salviniae*.

The effects on plants attacked by larvae of the two *Cyrtobagous* spp. differed considerably. Plants attacked by *C. singularis* became discoloured and the apical buds disintegrated. However, sections of rhizomes including nodes, survived attack by this species and retained the capacity for regrowth. In contrast, attack by larvae of *C. salviniae* resulted in death and sinking of rhizome sections.

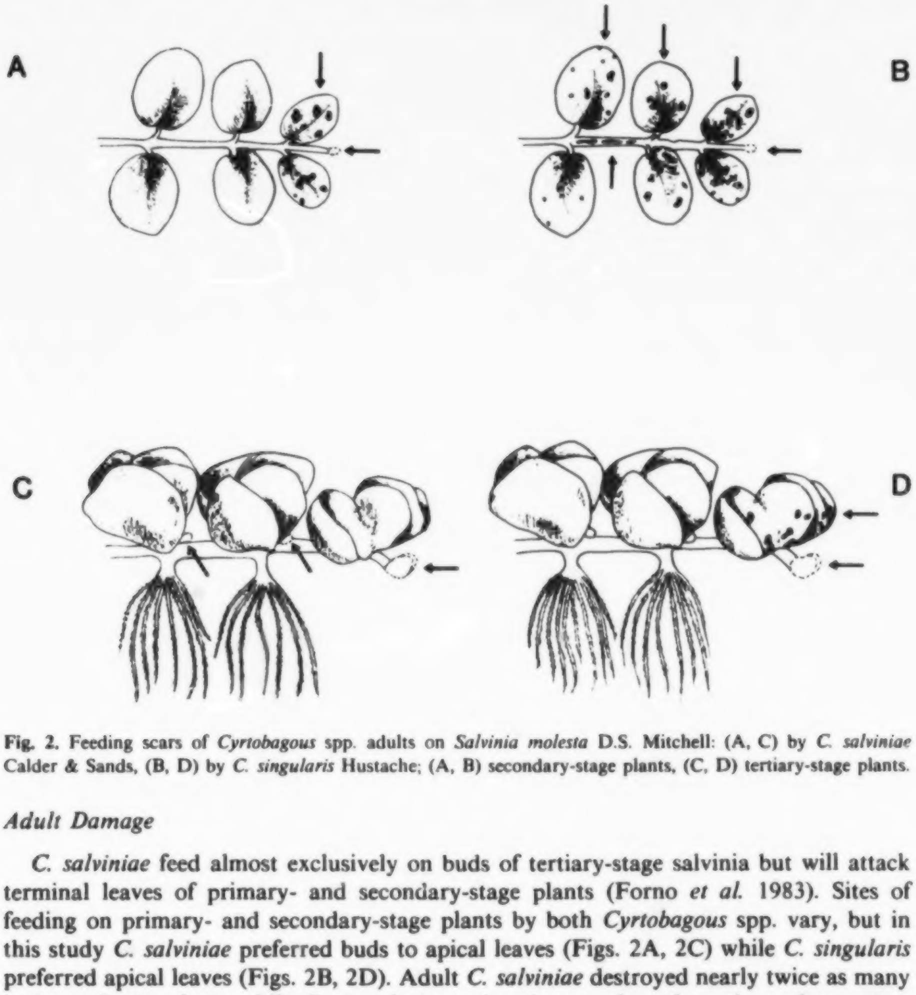

Fig. 2. Feeding scars of *Cyrtobagous* spp. adults on *Salvinia molesta* D.S. Mitchell: (A, C) by *C. salviniae* Calder & Sands, (B, D) by *C. singularis* Hustache; (A, B) secondary-stage plants, (C, D) tertiary-stage plants.

Adult Damage

C. salviniae feed almost exclusively on buds of tertiary-stage salvinia but will attack terminal leaves of primary- and secondary-stage plants (Forno *et al.* 1983). Sites of feeding on primary- and secondary-stage plants by both *Cyrtobagous* spp. vary, but in this study *C. salviniae* preferred buds to apical leaves (Figs. 2A, 2C) while *C. singularis* preferred apical leaves (Figs. 2B, 2D). Adult *C. salviniae* destroyed nearly twice as many buds as *C. singularis*, while *C. singularis* produced more than three times the number of scars on leaves as *C. salviniae* (Table 1). Moreover, while *C. salviniae* confined their attack on leaves to the apical pair, *C. singularis* frequently attacked pairs 2, 3 and sometimes 4 and 5. Further, while adult *C. salviniae* rarely fed on leaf petioles, *C. singularis* frequently did so, and produced a chain of scars in the aerenchyma of the internodes.

The Potential of Two Cyrtobagous *spp. as Biological Control Agents*

Harris (1981) stated that most agents used for the biological control of weeds stress, but do not kill the target weed. In this study the stress resulting from feeding by adults and larvae of the two *Crytobagous* spp. differed considerably. Room (1984) predicted that 50–75% destruction of buds of salvinia should halt growth of the weed, suggesting that adults alone, of both *Cyrtobagous* spp. are capable of affecting control. However, we suggest that the greater effect of *C. salviniae* from larvae destroying rhizomes and adults destroying more buds, may explain its success as a biological control agent for salvinia, where stress from attack by *C. singularis* has been relatively ineffective.

Table 1. Comparison of feeding by two *Cyrtobagous* spp. on *Salvinia molesta* (secondary stage).

Insect stage	Damage	*C. salviniae*	*C. singularis*
		(No./♀/day±SE)	
Adults (n = 10/sp.)	Buds destroyed	0.77±0.18	0.42±0.06
	Internode scars	0.63±0.24	4.32±0.48
	Leaf scars (<1mm)[1]	3.13±0.78	11.40±1.55
		(No./newly-emerged-pupation)	
Larvae (n = 30/sp.)	Buds destroyed	1.18±0.10	3.05±0.20
	Separate feeding sites	1.25±0.14	4.28±0.30

[1] Scars >1 mm result from attack on expanding buds.

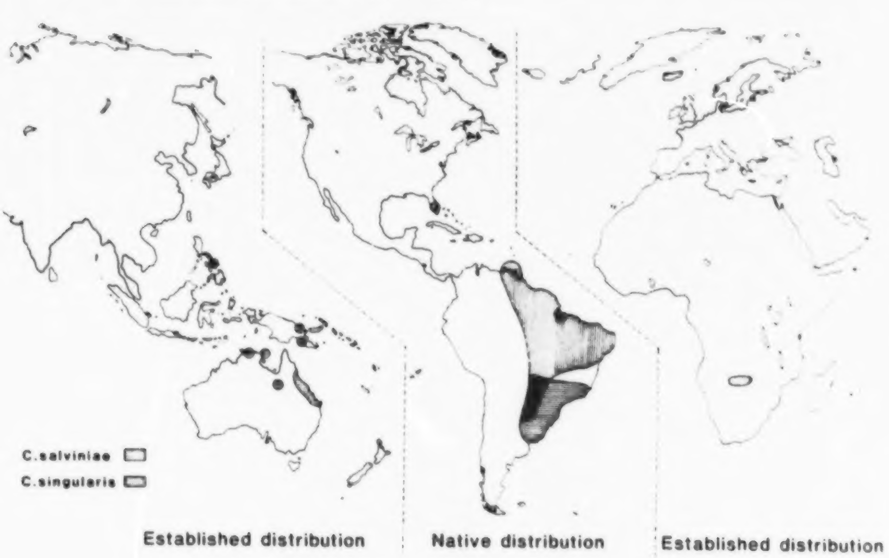

Fig. 3. Distribution of two *Cyrtobagous* spp.: 1984.

The two species share a common distribution over part of their natural range in South America (Calder and Sands 1985) and are now established on salvinia in several other countries (Fig. 3). When *C. singularis* was introduced to Botswana and Zimbabwe for control of salvinia (Bennett 1975), control of the weed was not achieved even though the weevil is now known to have established on *S. molesta* in the Caprivi region of southern Africa (Procter 1984). When contrasted with the success of *C. salviniae* in Australia (Room *et al.* 1981), we believe the performance of the two weevils can be attributed to subtle differences in their feeding behaviour. This study, which began to compare two populations thought to be biotypes, resulted in the discovery of two separate species, with different biological characteristics and potentials as biological control agents.

Acknowledgments

We thank Drs. F.D. Bennett and I.W. Forno for providing the original stocks of *Cyrtobagous* spp.

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Use of the Chinese Grass Carp, *Ctenopharyngodon idella*, in the Control of the Submerged Water Weed *Potamogeton pectinatus* in an Inland Lake in the Transvaal, South Africa

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Abstract

As a result of nutrient loads trapped in sediments of Germiston Lake, Transvaal, which was rehabilitated from acid pollution from gold mine dumps, the submerged aquatic weed *Potamogeton pectinatus* invaded the littoral zone of the lake, seriously threatening recreational use of the water body. Attempts at mechanical removal of the weed proved ineffective. Chemical control was not considered because of costs involved and the possible health hazard it might pose.

An indigenous warm-water weed-eating cichlid *Tilapia rendalli* introduced experimentally into the lake did not survive prevailing winter water temperatures below 10°C. The Chinese grass carp was then introduced which not only grew well but also succeeded in controlling the excessive growths of *P. pectinatus* in the lake within 18 months.

Utilisation de la Carpe Herbivore *Ctenopharyngodon idella* pour la Lutte Contre la Mauvaise Herbe Aquatique Submergée *Potamogeton pectinatus* dans un Lac de la Province de Transvaal, en Afrique du Sud

La libération des charges alimentaires enfouies dans les sédiments du lac Germiston de la province de Transvaal au cours de sa dépollution (il avait été acidifié par l'infiltration des résidus de mine d'or) a provoqué la prolifération de la plante nuisible aquatique submergée *Potamogeton pectinatus* qui a envahi les rives du lac et a ainsi gravement nui à l'utilisation récréative de la nappe d'eau. Les tentatives d'élimination mécanique de la plante nuisible ont été inefficaces. La lutte chimique n'a pas été prise en consideration compte tenu des coûts élevés et des dangers qu'elle risquait de poser pour la santé.

Un cichlidé herbivore indigène des eaux chaudes, *Tilapia rendalli*, a fait l'objet d'essais d'ensemencement, mais il n'a pu résister aux températures dominantes inférieures à 10°C de l'eau pendant l'hiver. La carpe herbivore *Ctenopharyngodon idella* a ensuite été introduite; ce poisson s'est non seulement bien développé dans le lac, mais y a également réduit la croissance excessive de *P. pectinatus* en 18 mois. Le rapport traite des possibilités de l'utilisation de ce poisson dans la lutte contre les mauvais herbes aquatiques en Afrique du Sud.

Introduction

Shifts in population densities in South Africa towards the more industrialized regions, largely confined to the Transvaal, where many gold mines are concentrated, has led to increased dependence there of man on impoundments for domestic, industrial and recreational needs. Germiston Lake near Johannesburg, *c.* 58 ha in size, with a relatively small catchment area of just over 1100 ha receives much of its water through stormwater drains. Apart from occasional minor pollution which occurred in the lake from effluents of metal industries, the quality of the lake water prior to 1969 was largely affected by seepage of highly mineralized acid water from nearby worked-out mine and ash dumps. Pollution of the lake water by mine and industrial effluents, which prohibited fish life for more than eighty years, dates back to the turn of the century when the lake was originally used to receive water and mineral-rich sludge pumped from the then-active working, but now defunct, Simmer and Jack gold mine.

In 1969 the first steps were taken by the Department of Zoology of the Rand Afrikaans University in collaboration with the municipal authorities of Germiston to rehabilitate the lake from pollution (Vermaak 1972). At that time, prior to remedial measures being taken to rid the lake from pollution, the pH of the lake water (largely affected by concentrations of sulphuric acid in seepage water from mine dumps), fluctuated mainly between 3.5 and 4.5. Mineral loads in the water contributed much to high conductivities recorded which exceeded 2500 μS/cm on occasions (Table 1). Similarly, values obtained for total Mg and Ca hardness as well as those for chlorides and sulphates were all exceptionally high (1969–70 results, Table 1). First steps in recovery of the lake from pollution were taken in 1969–70. The various sources of mineral and organic pollution were first located (Vermaak 1972) and where possible, immediately eliminated by the City Engineer's, Parks and Recreation and Health Departments of the municipality. Seepage water emanating from the mentioned mine and ash dumps were diverted into a canal around the lake. To render the lake water more alkaline, more than 10^6 *l* NaOH was added, followed by the dispersal into the lake of *c.* 59 t of agricultural lime. Largely as a result of investigations by Vermaak (1972) and subsequent monitoring of conditions in the lake, no further serious pollution occurred. Due to strict control measures by municipal authorities (which followed elimination of major sources of pollution) but also as a result of periodic influx of rainwater into the lake, mineral loads in the lake water, as reflected by conductivity and related parameters (Table 1), rapidly declined by almost 40% within the first year of recovery. Since 1970 a progressive decrease in the mineral loads of the lake took

Table 1. Some physico-chemical parameters of the water in Germiston Lake based on mean values obtained at 8 sampling localities during the various seasons of 1969-1970, 1978 and 1983. All values except pH and conductivity, in mg/l; analyses done according to Apha (1977).

Parameters	1969-1970		1978		1983	
	Mean	Range	Mean	Range	Mean	Range
pH	–	3.5-6.9	–	7.8-9.2	–	7.8-8.8
Conductivity (μS cm^{-1})	2009	1644-2580	982	922-1061	793	700-880
DO	6.9	6.5-7.6	9.8	6.1-12.4	–	–
BOD	1.7	1.1-2.4	2.4	1.1-4.4	–	–
Total Alkalinity	20	11-31	73	65-82	–	–
Total Hardness ($CaCO_3$)	1074	890-1290	429	403-460	329	300-347
Mg-Hardness ($CaCO_3$)	395	310-505	165	144-190	–	–
Ca-Hardness ($CaCO_3$)	678	580-785	264	247-785	–	–
Cl^-	122	100-153	87	80-98	72	62-85
$SO_4^=$	978	886-1094	297	280-320	272	240-320
SRP ($PO_4^≡$)	0.05	0-0.30	0.09	0.05-0.20	0.11	0.003-0.30
NO_3–N	2.76	2.2-3.6	1.59	1.45-1.75	0.90	1.50-1.00

place accompanied by dramatic increases in pH-values, which in 1978 and 1983 constantly fluctuated above 7 (Table 1).

Values for dissolved oxygen recorded in the lake, which ranged between 6.5 and 7.6 in 1969, began to fluctuate more during the subsequent years when water quality conditions began to improve. This was accompanied by increased algal blooms, especially during winter and the rapid development of submerged aquatic weeds.

Introduction of Fish into Lake

With the recovery of the lake water from pollution in 1970 certain fish species were introduced which could utilize the benthic macro-invertebrate fauna as well as the filamentous algal growths which covered the lake substrate. As a result of the occurrence of large numbers of chironomid larvae (Diptera: Chironomidae) and their flying adult stages which became a nuisance to people dwelling nearby, the benthic-feeding common carp *Cyprinus carpio* and Vaal river yellowfish *Barbus holubi* were released into the lake during 1971 followed by the largely algal feeding cichlid *Tilapia sparramanii*. With the exception of the yellowfish, which requires running water and a gravelly substrate to spawn, both the other two species reproduced so successfully after one year that two predators (namely the African sharptooth catfish, *Clarias gariepinus*, and the largemouth black bass, *Micropterus salmoides*) had to be introduced to control their numbers. Of the latter two species, *C. gariepinus* also spawned successfully in the lake. Since 1973 the lake developed into a popular angling resort.

The Problem of *Potamogeton pectinatus* L. (Potamogetonaceae)

At the time of its recovery from pollution in 1971–72 only three species of aquatic macrophytes were observed to occur in appreciable densities in the lake; namely *Phragmitis communis* Trin. (Gramineae), which largely occurred around the southwestern perimeter of the lake, *Scirpus lacustris* L. (Cyperaceae) and *Lagarosiphon major* (Ridley) Moss (Hydrocharitaceae) (Vermaak 1972). In view of the improvement of water quality conditions, it was anticipated that a greater variety of aquatic organisms would appear and proliferate in the lake. It was also expected that the thick deposits of nutrient-rich sediments might facilitate increased growths and expansion in the lake of the already mentioned isolated stands of *Scirpus* and *Lagarosiphon*. In 1972 a small colony of *Potamogeton pectinatus* was observed in the lake. Since then and over a period of 3 yrs this species invaded the entire littoral zone of the lake, replacing almost completely *Scirpus* and *Lagarosiphon*. By 1978 the estimated wet biomass of *P. pectinatus*, based on seasonal quantitative transect studies on distribution of this weed in the lake (Fig. 1), amounted to 1329 t during summer with a winter maximum of 95 t (Vermaak *et al.* 1981). Seasonal biomass ratios of this weed was 1:2:4:8 for spring, winter, autumn and summer 1978, respectively. Due to clarity of the lake water column and active light penetration to the bottom of the lake at depths exceeding 3 m, densities in stands of *P. pectinatus* were still comparatively high at distances of 50 m and more from the shoreline (Fig. 2; data for 1978).

Steps to Control *P. pectinatus*

The progressive and rapid invasion of the lake by *P. pectinatus* seriously threatened effective management of the lake since 1973 and also made it virtually impossible for large portions of it to be used for water sport and recreation such as skiing, yachting and angling. Steps to combat the infestation of this weed were first taken by the Parks

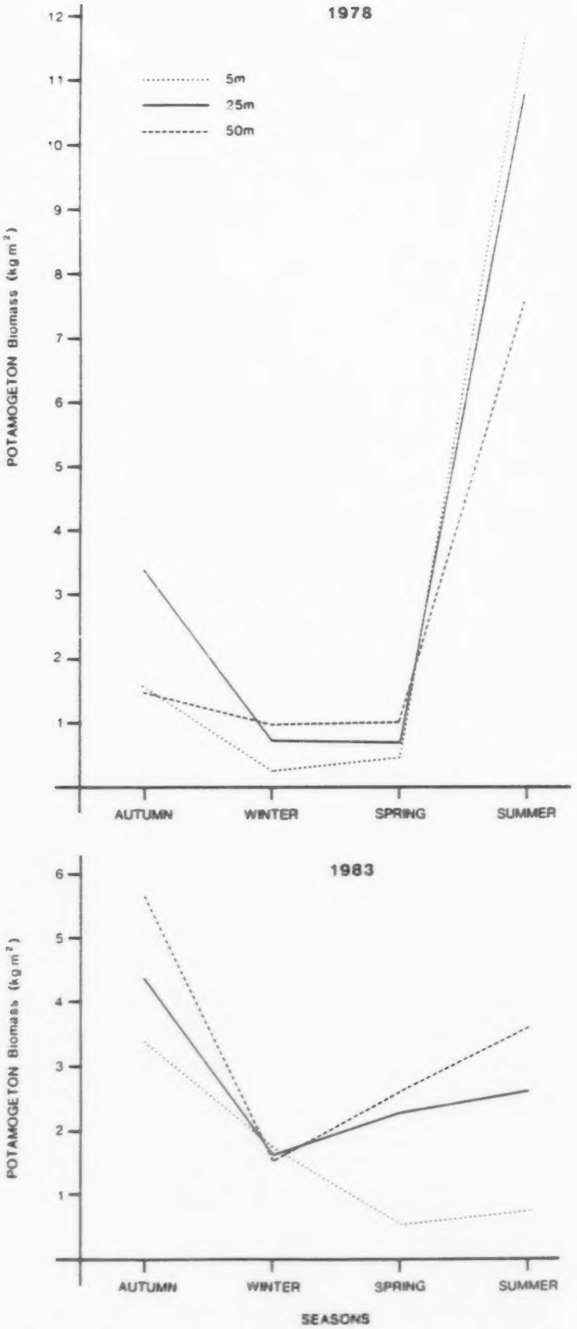

Fig. 1. Comparison of mean wet biomass values (kg/m^2) for *Potamogeton pectinatus* L. across transects at distances of 5, 25 and 50 m from the shore at eight localities in Germiston Lake for the various seasons of 1978 and 1983.

and Recreation Department of the municipality in July 1973 when a floating Wilder underwater weedcutter was purchased for mechanical removal of the plant at depths of up to 2 m below the water level. Despite acquisition of a second weedcutter in February 1975 it was still not possible to control this weed effectively. It was also found that annual operational costs to cut and remove the weed from the lake area became prohibitive, increasing to more than SA R100,000. From results obtained on mechanical removal of this weed it was clear that only limited success would be obtained controlling this weed in this way despite the high costs and efforts involved.

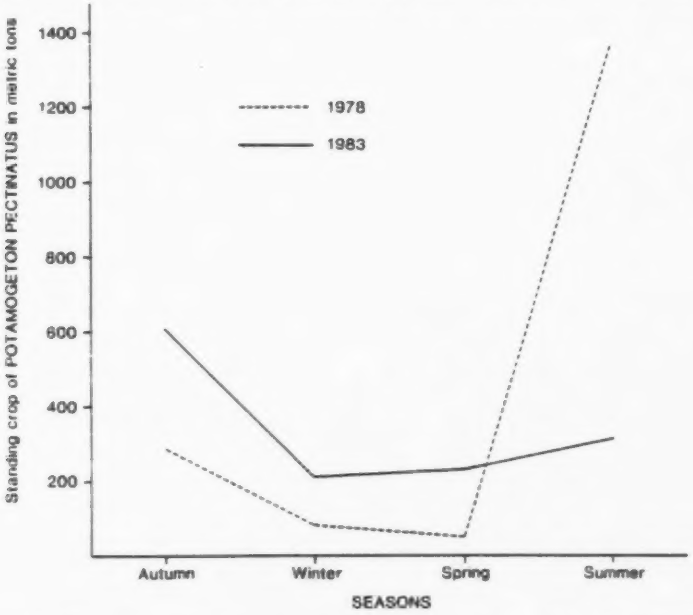

Fig. 2. Comparison of standing crop of *Potamogeton pectinatus* L. in Germiston Lake for the various seasons of 1978 and 1983.

Use of herbicides by research workers in South Africa and elsewhere for successful control of floating weeds such as water hyacinth, *Eichhornia crassipes* (Mart.) Solms. (Pontederiaceae) (Wild 1956; Robinson 1965; Van Donselaar 1968; Scott *et al.* 1979) was not considered, as even higher concentrations of weed killer would be needed for control of submerged weeds, and it was feared that levels of herbicide required to control *P. pectinatus* in Germiston Lake could be harmful to other aquatic organisms. Also, the danger existed that the levels of herbicide residues released into the water might exceed limits specified by the Department of Health of South Africa.

The possibility of using an indigenous weed-eating freshwater fish to control *P. pectinatus* was also considered as an alternative to mechanical removal, or use of herbicides, which was left as a last resort should all other attempts to control *P. pectinatus* fail. Apart from *T. sparrmanii*, which is omniverous but primarily an algal feeder (Crass 1964; Jubb 1967), none of the other already-mentioned fish species introduced into the lake were able to utilize *P. pectinatus* as food. The only indigenous South African freshwater fish known to actively feed on aquatic macrophytes is the red-chested tilapia, *T. rendalli* (Jubb 1967; Potgieter 1974; Bruton *et al.* 1982). This fish was released experimentally in the lake during 1973, in a cage enclosure at a density of 1 fish/m^2. At this density, *T. rendalli* was found to control *P. pectinatus* stands successfully during summer. Being a warm-water fish, however, it could not survive the colder, winter water temperatures which declined below 10°C in the lake. Mass mortalities occurred when the mean water temperatures declined below 14°C.

Introduction of the Chinese Grass Carp, Ctenopharyngodon idella *Val. (Cyprinidae)*

Since none of the local indigenous fish species were able to control effectively excessive growths of submerged aquatic weeds under low temperature water conditions (Kruger and Brandt 1975), the Chinese, phytophagous, cold temperature tolerant, grass carp *C. idella* was first imported into South Africa from Malaysia by the Natal Parks and Fish Preservation Board for the purpose of investigating this fish in aquatic weed control programs. These fish, kept at the Umgeni Fish Hatchery in Natal, were spawned artificially with limited success in 1974. Some of these fish so produced were used in some experimental control of aquatic weeds in Natal. In 1975 a second group of 330 grass carp juveniles were imported from Mindelaltheim, West Germany, by the Marble Hall Fish Research Station of the Division of Nature Conservation of the Transvaal Provincial Administration (DNC). These fish were grown to maturity and successfully spawned with the aid of carp pituitary gland extract (*PGE*) and human chorionic gonadotropin (*HCG*) in 1977 (Schoonbee *et al.* 1978). Since then, methods for large-scale artificial spawning of this fish species were perfected under local conditions at various fish hatcheries in southern Africa (Brandt and Schoonbee 1980; Schoonbee and Prinsloo 1984).

After obtaining permission from and in co-operation with the DNC, grass carp juveniles, spawned in 1981 at the Umtata Fish Hatchery of Transkei and grown to an average size of 26.9 g, were transported in oxygen-filled plastic bags to the lake. A total of 7000 juveniles were released on 27 November 1982 in an open cage, 50 × 20 m, sunk into the lake substrate and isolated from the rest of the lake by 10 mm nylon mesh screen as enclosure. After 6 wks acclimation, the fish were released into the lake. A set of fine mesh steel screens prevented the fish from leaving the lake at its point of outflow. An anticipated 30% mortality was allowed for as the fish were of large enough size not to be caught so easily by fish-eating birds such as cormorants which frequent the lake in large numbers.

Observations on Growth of Grass Carp in Germiston Lake

Gill nets were used to sample the fish on two occasions after their release, namely after 298 days (21 September 1983) and again after 436 days (11 February 1984) towards the end of the 1983–84 summer period. No serious mortalities of grass carp released into the lake were observed. Results obtained on growth performance of the fish based on number caught are represented in Table 2 and Fig. 2.

During the first 298 days after release of grass carp in the lake (which included winter 1983), fish (mass 1187 g) were found to grow at an average rate of 3.9 g/day. In a further 138 days and at a mean mass of 4023 g the growth rate of the grass carp over the 1983–84 summer season amounted to 10.18 g/day (Table 2; Fig. 1).

Comparison of P. pectinatus *Biomass in 1983 with that of 1978*

To determine possible effects of grass carp on biomass of *P. pectinatus* in 1983, procedures followed in collection and processing of the weed were the same and at the identical localities, as well as along the same transects, as those for the 1978 surveys

(Vermaak *et al.* 1981). A comparison of the results obtained for 1983 with those of 1978 (Fig. 1) showed that for autumn, biomass values at all three distances from the lake shore, were in each corresponding case higher during 1983. These findings are in agreement with observed increases in densities of *P. pectinatus* during 1980–83 and substantiate the problems experienced by people using the lake for recreation. The results also indicated that the young grass carp still could not cope successfully at that stage in controlling the weed. A similar situation existed during winter with the biomass of *P. pectinatus* still being higher than that of 1978. A dramatic change occurred, however, during spring and summer of 1983, when not only a drastic increase in the size of the individual grass carp was observed, but the effective and spectacular control of otherwise luxurient growths of *P. pectinatus* of previous years, occurred. Where the mean summer biomass values for *P. pectinatus* fluctuated between 7.6 and almost 12 kg/m^2 during 1978, this was reduced to vary betwen 0.8 kg/m^2 (5 m from shore) and 3.6 kg/m^2 (50 m from shore) for 1983. The sharp reduction and eventual disappearance of *P. pectinatus* from the upper layers of the lake water since summer 1983 is further demonstrated by figures calculated for standing crop of this weed for the corresponding seasons of 1978 and 1983 (Fig. 2). Here again it can be observed that during the initial months after release of grass carp, the estimated *P. pectinatus* biomass for 1983 compared with 1978 were still higher by between 50 t and 150 t, respectively (autumn and winter, Fig. 2). However, between spring and summer 1983, when the estimated biomass of the grass carp ranged between 360–480 kg/ha, this fish was able to control the growth of *P. pectinatus* completely in Germiston Lake. Since release of grass carp in Germiston Lake in November 1982 it has not been necessary to use any other method of weed control.

Table 2. Biomass (g) and fork length (cm) measurements of grass carp, *Ctenopharyngodon idella* Val. at the time of introduction, after 298 and 436 days respectively, in Germiston Lake[1].

Date	*n*	Fish biomass (g)			Fork length (cm)		
		x	Range	S.D.	*x*	Range	S.D.
27-11-82	121	26.9	5.3-70.2	± 14.5	11.8	7.8-17.20	±2.2
21-09-83	10	1187.0	724-1836	±301.0	40.5	36.00-48.20	±3.5
06-02-84	10	4022.5	3351-4795	±440.0	58.6	55.00-60.90	±1.8

[1] First introduction of fish into cages in lake.

The Problem of *Bothriocephalus gowkongensis* (Bothriocephalidae)

Even though strict precautionary measures were taken to prevent importation of diseases with grass carp into South Africa, indications are that an outbreak of *B. gowkongensis* at the Transvaal Provincial Fisheries Research Station, at Marble Hall amongst the common carp *C. carpio* was due to an original infestation of grass carp brought in from West Germany (Brandt *et al.* 1981). This parasite which uses a cyclopoid copepod as intermediate host for part of its larval development was also recorded from other cyprinid fish at other localities in the Transvaal. An effective treatment against the parasite for pond fish was worked out using the cestocide Lintex (2′,5′-dichloro-4′-nitrosalicylamide) a Bayer niclosamide preparation (Brandt *et al.* 1981).

Concluding Remarks

The use of the Chinese grass carp, *C. idella*, to control the aquatic weed *P. pectinatus* in Germiston Lake, Transvaal, has been achieved within a period of 18 months and indications are that this fish will be able to stabilize growth of this weed to acceptably low levels providing a certain number of the fish can be maintained in the lake in the future. Further investigations will, however, have to be made on the possible impact of *C. idella* on the rest of the lake ecosystem. Such information will be valuable in any future use of this fish species if similar weed control programs in the Transvaal may be contemplated. The considerable impact of a relatively small number of grass carp on the density of *P. pectinatus* in the lake clearly points towards the care that must be taken not to overstock a water body with this fish in the event of a control program. A knowledge of the standing crop and the preference of the fish for a particular weed that needs to be controlled is of the utmost importance.

Acknowledgments

This paper is dedicated to our colleague, the late Dr. J.F. Vermaak, who was intimately involved in the rehabilitation of Germiston Lake and who died tragically during an accident on 22 October 1983. Our sincerest thanks are due to the Municipality of Germiston for their generous financial support which made this study possible and to the staff of the various Municipal Departments, who played an active role in the elimination of the various sources of pollution. The financial assistance of the Victoria Lake Yacht Club is also hereby gratefully acknowledged. The Division of Nature Conservation of the Transvaal Provincial Administration is thanked for allowing us to use the Chinese grass carp for the control of *P. pectinatus* in Germiston Lake. The Department of Zoology of the University of Transkei is thanked for the provision of grass carp juveniles which were spawned at the Umtata Fish Hatchery for the purpose of this investigation. Lastly this work was made possible by equipment and laboratory facilities provided through the Department of Zoology of the Rand Afrikaans University.

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Towards Biological Control of Salvinia in Papua New Guinea

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Abstract

The aquatic fern *Salvinia molesta* is causing major problems in > 500 km^2 of waterways in the Sepik River basin, Papua New Guinea. Approximately 1200 adult *Cyrtobagous salviniae* were introduced as biological control agents in 1982. Field establishment was achieved only when the nitrogen content of salvinia at the initial release site was raised by application of urea. Evidence was obtained that feeding damage caused by *C. salviniae* modifies the host plant in favour of the insect by raising nitrogen levels. A critical density of weevils may be required to trigger conditions favourable for a population explosion. *C. salviniae* is now well-established in the Sepik basin and some 500,000 adults had been distributed to 60 sites by mid-1984. The insect is most successful on thin, mobile weed mats and is already providing control in several lakes.

Lutte Biologique Contre Salvinia a Papua, en Nouvelle-Guinée

La fougère aquatique *Salvinia molesta* suscite de graves problèmes sur une superficie de plus de 500 km^2 du bassin de la rivière Sepik à Papua, en Nouvelle-Guinée. Environ 1200 adultes d'une espèce de charançon *Cyrtobagous salviniae*, ont été libérés comme agents de lutte biologique en 1982. Les insectes ne se sont établis que lorsque la teneur en azote des *Salvinia* dans le site initial d'introduction des insectes a été augmentée par l'application d'urée. D'après les observations, les dommages causés par *C. salviniae* entraînent une augmentation des concentrations d'azote de la plante hôte, ce qui favorise les insectes. Une certaine densité de charançons peut être critique pour créer des conditions favorables à une explosion de la population. *C. salviniae* est actuellement bien établi dans le bassin Sepik, et au cours des premiers mois de 1984, quelque 500,000 adultes ont été introduits en 60 sites. L'insecte réussit mieux sur les minces couches de plantes nuisibles mobiles et assure déjà une lutte efficace dans plusieurs lacs. Pour les couches de plantes nuisibles fortement colonisées par une végétation flottante secondaire, il sera peut-être nécessaire d'avoir recours à des méthodes de lutte intégrée, c'est-à-dire commencer par un traitement herbicide et ensuite introduire *C. salviniae*, pour empêcher la régénérescence de *S. molesta*.

Introduction

Salvinia molesta D.S. Mitchell (Salviniaceae) is a free-floating aquatic fern which originated in S.E. Brazil (Forno and Harley 1979). Man has distributed the plant widely through the tropics and subtropics. The plant can double in weight, numbers of ramets and leaf area in as little as 2.2 days (Farrel 1979), and its ability to cover areas of still water rapidly has caused it to be regarded as one of the world's worst aquatic weeds.

The exact time and place of introduction of salvinia to Papua New Guinea (PNG) are not known. Recent oral history suggests that it was taken to the Sepik River from the nearby coastal town of Wewak in 1971-72. The Sepik River rises near the border between PNG and Irian Jaya and for most of its 1200 km course meanders west to east through a wide alluvial flood plain. In its middle and lower reaches, the river is up to 500 m wide and 35 m deep. Hundreds of oxbow and shallow depression lakes and lagoons are associated with the river. These vary in size from a few ha to the 250 km^2 Chambri Lake. Depending on their age, and degree of useage by local people, the lagoons may be connected to the mainstream by permanent or seasonal channels.

The lives of Sepik villagers centre on the use of these waterways for fishing, access to garden areas and sago palm swamps (the major carbohydrate source) and to more distant facilities such as markets, schools and hospitals. By forming thick floating mats, salvinia interferes with or prevents, movement of canoes and outboard-powered boats, seriously disrupting most aspects of traditional, subsistence lifestyles. In addition, the plant interferes with economic activities such as trade in crocodile skins and sale of artifacts to tourists. Mitchell (1979) and Thomas (1979) recommended, *inter alia*, that an integrated approach with biological control as the major component would provide the only economically viable long-term solution. In 1981 a joint UNDP/FAO/PNG Government project was set up to develop cost-effective management of salvinia in PNG.

By the end of 1980 the plant had spread through 500 km^2 of waterways with some 200 km^2 of water surface covered by weed mats. During 1981 one of us (Thomas) carried out trials with herbicides and the use of booms, while Room (1981) reported on the prospects for extending to PNG techniques for biological control of salvinia being developed in Australia. Although the short-term results of chemical control were spectacularly effective, regrowth from plants sheltered by marginal vegetation, and the consequent need for repetitive spraying made chemical control alone, an uneconomic proposition. Mechanical or physical control was found to have only limited application.

Control of salvinia on Lake Moondarra in central Queensland, Australia, was achieved in 1981 using a weevil, thought at the time to be *Cyrtobagous singularis* Hustache (Coleoptera: Curculionidae) (Room *et al.* 1981). Subsequent investigations (Sands 1983) showed the weevil to be a previously undescribed species, *Cyrtobagous salviniae* Calder & Sands (Calder and Sands 1985), and all subsequent references to *Cyrtobagous* in this paper are to this species. The biology and feeding habits of *Crytobagous* have been described by Forno *et al.* (1983) and Sands *et al.* (1984). Another insect, *Samea multiplicalis* (Guenée) (Lepidoptera: Pyralidae), had also been released in Australia (Room *et al.* 1984) but *Cyrtobagous* appeared to have greater potential and it was decided to import this insect into PNG first.

Introduction and Establishment of *Cyrtobagous salviniae*

The data summarised here are presented in detail in Room and Thomas (1985).

The first importation of *C. salviniae* into PNG consisted of 590 adults collected from Lake Julius, central Queensland, where the weevil had been established previously. The 50 ha Binatang Lagoon, 10 km east of Angoram (4.04°S 144.04°E) was selected for the first release. It was completely covered by salvinia and a few small sudd islands. However, in contrast to Lake Moondarra, the salvinia in Binatang Lagoon appeared yellowish, suggesting a nutrient deficiency. In February 1982, two 2 × 2 m floating cages, similar to those described by Room *et al.* (1981) were placed over salvinia in the lagoon and several days later, 285 adult *C. salviniae* were released into each cage. In an attempt to overcome the possible nutrient deficiency, a plastic bag containing 2 kg of NPK fertiliser was pierced in several places and hung just below the water surface in each cage. The bags were recharged on 3 June 1982.

No regular sampling was carried out as we wished to keep disturbance and removal of salvinia (and insects) to a minimum. There was little apparent damage to the salvinia in the cages by September 1982, despite there having been time for four generations of the insect since introduction (Forno *et al.* 1983).

Samples extracted with Berlese funnels (Boland and Room 1983) in early September suggested that there were only *c.* 20 adults in each cage, mostly concentrated around the bags of fertiliser. There was no evidence of predation or parasitism and comparison with a wide range of Australian release sites (Room *et al.* 1984) indicated that climatic factors were not likely to be limiting. Salvinia 30 m from the cages had a mean nitrogen content for the period February–September 1982 of 0.96% dry weight ($n = 24$). This contrasted with an average of 1.71% N ($n = 7$) in Lake Moondarra, where *C. salviniae* destroyed 80% of salvinia in similar cages in only seven months (Room *et al.* 1981).

Effects of Nitrogen on Weevil Populations

We suspected that establishment of the weevils in Binatang Lagoon was being hampered by low N levels. In late September 1982, therefore, a further 296 *C. salviniae* from Lake Julius and a second bag of NPK fertiliser were added to each cage. Additional N was supplied each week until mid-March 1983 by spraying 25 g urea in 200 ml water on the salvinia in each cage.

By mid-November, 1.5 generations later, 90% of salvinia buds in the cages had been damaged and Berlese funnel samples from the cages showed that the *C. salviniae* population had more than doubled. Over the next 6 wks, quantities of salvinia containing all stages of *C. salviniae* were removed from cages and placed just outside them. Fresh salvinia was placed inside the cages to ensure an adequate food supply for the remaining insects. Salvinia heavily damaged by *C. salviniae* turned dark green, suggesting high N levels, before turning brown and rotting. Average N content of salvinia inside the cages during fertilising was 1.75% ($n = 4$), in contrast to 1.10% ($n = 30$) 30 m from the cages.

To test the apparent effect of applying urea, a series of experiments was started in other Sepik lakes. *C. salviniae* was released onto salvinia receiving: (a) no fertiliser; (b) urea; and (c) urea + superphosphate. Developments were monitored weekly. Results to date, and results of similar experiments in Australia (Room *et al.* 1985), clearly indicate that raising the concentration of N in salvinia from < 1% to near 1.5% dry weight significantly increased the rate of *C. salviniae* reproduction. Conversely, applying superphosphate in addition to urea appeared to have no, or even a slight negative, effect.

Still further evidence for the importance of N content of salvinia to its biological control agents has been demonstrated by the studies of Sands *et al.* (1984) and Taylor (1984). These workers have shown that high levels of N cause faster development of larvae and increases in fecundity of both *C. salviniae* and *S. multiplicalis.*

Contrary to expectations, the population of *C. salviniae* in Binatang Lagoon continued to thrive as it slowly expanded away from the cages and the fertilised salvinia. In addition, regenerating salvinia was usually darker green than nearby, relatively undamaged material. This suggested that feeding by *C. salviniae* may modify the host plant to the insect's advantage. Destruction of buds precedes more extensive damage to older tissues. This may reduce competition for nutrients between surviving buds, while at the same time making more nutrients available from an increase in decaying plant material and insect frass.

Further evidence in support of this hypothesis came from two sources. In the fertiliser experiments, N levels in the control remained very similar to background N until emergence of the F_1 generation of *C. salviniae* produced a sudden increase in damage, whereupon N levels suddenly rose to the level in the +N and +NP treatments and remained at that level until just before the plant material died and sank (Fig. 1). In Binatang Lagoon (Fig. 2), tissue samples from heavily damaged plants close to the cages, consistently had higher N levels than relatively undamaged plants 30 m away. This trend continued until October–November 1983 when damage levels at 30 m became similar to those near the cages and the difference in N levels became much less pronounced.

In February 1983, 107 adult *C. salviniae* were extracted through Berlese funnels from 3 kg of salvinia from the cages and were released onto a thick salvinia mat on Gerehu Lake, near Port Moresby. The lake receives sewage effluent and provided an opportunity to assess the performance of *C. salviniae* under consistently higher N conditions than would normally be found in the Sepik.

Also in February 1983, 6 kg of salvinia containing *c.* 200 adult *C. salviniae* from the cages was placed among salvinia growing in seasonally flooded sago swamp adjacent to the channel connecting Binatang Lagoon to the Sepik River. This salvinia was exposed to silt-laden water flowing through the swamp at the peak of the flood season and could be expected to experience high nutrient levels. On 13 May 1983, a single sample of salvinia from the sago swamp contained 1.54% N compared with a routine sample, 30 m from the Binatang Lagoon cages, which contained 0.89% N. Patches of heavy *C. salviniae* damage and large numbers of adults were present in the sago swamp. These could only have developed from the insects released there in February and in only two generations the population density had far exceeded that in Binatang Lagoon.

Field Distribution of *Cyrtobagous salviniae*

The population explosion of insects in the sago swamp persisted from May until August when the last pockets of salvinia dried out with the falling flood level. During this period, some 100,000 adults and many more eggs, larvae and pupae were distributed to other lagoons in the Angoram area. Infested salvinia was placed in jute sacks and carried by boat to new sites in the Angoram area. A subsample of 2 kg was taken from each sack and *C. salviniae* were extracted using Berlese funnels to estimate the number of adults released at each site (generally 100–300 kg of salvinia containing 2000–12,000 adults). The live adults extracted from subsamples were flown to Ambunti, 150 km up river from Angoram, for release near the upstream limit of the salvinia infestation. Approximately 6000 adults were distributed in this fashion.

By November 1983, *C. salviniae* populations in lagoons near Angoram had developed sufficiently to allow further redistribution in the vicinity and *c.* 150,000 adults were moved to Ambunti by flying sacks of infested salvinia there for redistribution by boat. Attempts to drop infested salvinia into lagoons from a fixed-wing aircraft were unsatisfactory because the material spread over too wide an area. In response to radio appeals, a number of Sepik villagers carried infested salvinia back to their own lagoons.

By May 1984, some 500,000 adults had been distributed to 60 Sepik lagoons and establishment had been confirmed in half of these. The delay between release and what can be considered permanent establishment is not easy to assess with accuracy. In some lagoons assessment has been complicated by several releases being made at intervals and at other sites by the irregularity of visits. On Gerehu Lake, for example, the insects had multiplied sufficiently to cause discolouration of salvinia at the release site after $3\frac{1}{2}$ months. In the Sepik, four months elapsed between the earliest release on Imbuando Lagoon and the discovery of a widespread breeding population. Elsewhere in the Sepik

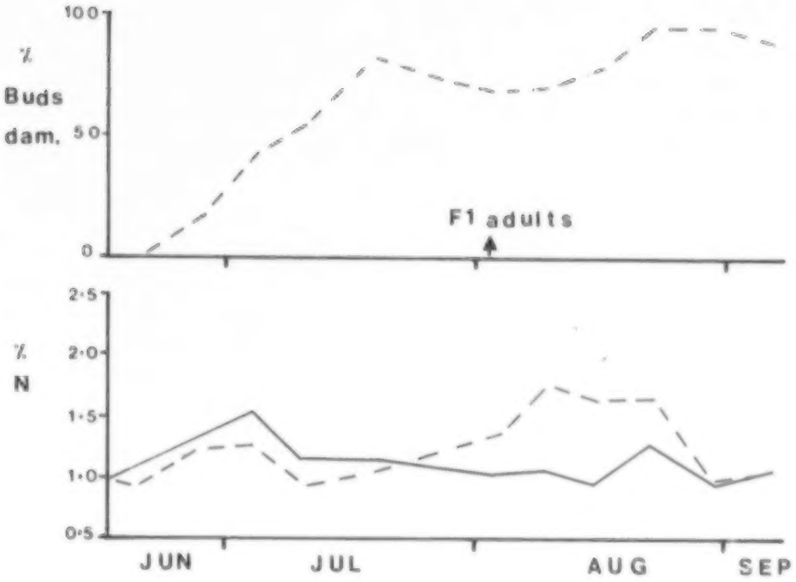

Fig. 1. Percent of buds damaged and % nitrogen dry weight in *Salvinia molesta* D.S. Mitchell with (– –) and without (—) attack by *Cyrtobagous salviniae* Calder & Sands.

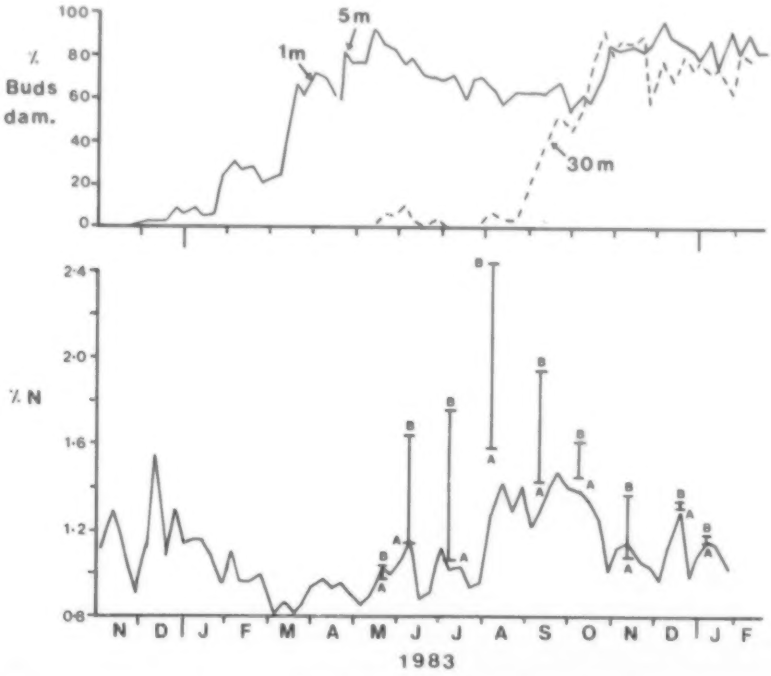

Fig. 2. Percent of buds damaged 1, 5 and 30 m from the cages in Binatang Lagoon and % nitrogen dry weight 30 m from the cages (continuous line and A) and 5 m from the cages (B). Continuous line: samples of four youngest nodes/plant; A & B: samples of two youngest nodes/plant.

region, establishment has taken from three to nine months, with an average of about five months. The Gerehu release of 107 adults has been the smallest number of adults to have established in PNG. It is not known whether such a low number would suffice under the lower nutrient conditions in the Sepik.

Effects of *Cyrtobagous salviniae*

The performance of *C. salviniae* has varied considerably according to the nature of the salvinia infestations. In Binatang Lagoon, the insects moved away from the cages in a 'wave' (Fig. 2). The population close to the cages peaked in May 1983, then decreased, presumably as adults dispersed in search of food. This allowed damaged salvinia to regenerate to some extent and the insect population built up once more. In November 1983 there was another peak of activity both close to and further from the cages. Adult numbers reached *c.* 20/kg salvinia, with bud damage at *c.* 90%. Routine samples were only taken up to 30 m from the cages but it was apparent that insects were present on open mat through at least 75% of the lagoon. There was no indication of significant attack on salvinia which had been colonised by sudd vegetation. By May 1984 insects were present throughout the lagoon, open mats of salvinia had disappeared and sudd islands covered no more than 50% of the water surface.

Gerehu Lake provides an even more extreme example of the apparent reluctance of *C. salviniae* to disperse. In December 1983, 10 months after release, the insects had caused a well-defined patch of damage up to 20 m from the release site. Most of the damaged material was waterlogged and rotting, being held afloat only by the compaction of the very thick mat. No sign of insect activity could be found beyond 5 m from the obvious 'invasion front'. The complete immobility of the weed mat and its unusual thickness presumably ensured that the expanding insect population was continually presented with a fresh food supply. A similar development has occurred on Panau Lagoon in the Sepik region where three separate releases on a thick, stationary mat, have resulted in three discrete patches of *C. salviniae* damage. Room *et al.* (1984) report the same phenomenon from a very thick mat at Kaban in Australia.

The 370 ha Imbuando Lagoon presents a complete contrast to the sites discussed above. In May 1983, when salvinia cover was 80%, 15,000 adult *C. salviniae* were released into the centre of the open mat. By September 1983, mainly as a result of a cycle of partial flushing and regeneration, cover had fallen to 50% and the weed mat was extremely mobile. Low level *C. salviniae* damage was present throughout the lagoon. From September onwards the river began to rise, precluding any further significant flushing. By the beginning of November, bud damage had reached 50% and one month later exceeded 90% through the whole weed mat. Since that time the mat has turned progressively brown and has sunk. By May 1984 the lagoon was completely clear of salvinia with the exception of small, damaged plants confined to the marginal emergent vegetation. Most of the other sites in the Sepik region where *C. salviniae* has established appear to be following a similar pattern.

Discussion

Experience in the Sepik region suggests that *C. salviniae* will perform best on single layer, mobile weed mats. The insects rapidly become evenly distributed by movement of the weed mat resulting in uniform damage over the whole lagoon. Consequently, when food availability falls, the insects have nowhere to go and a high level of feeding pressure is maintained, resulting in destruction of the weed mat. In Imbuando, this pressure has become so great that the small sudd islands in the lagoon have also been destroyed. Whether or not this will happen in lagoons such as Binatang remains to be seen.

Reasons for avoidance by *C. salviniae* of sudd islands are not clear. Preliminary results suggest that thicker mats, whether or not colonised by sudd plants, are lower in N than thin mats from the same lagoon. This could be a result of increased competition and difficulties of root contact with water. On Gerehu Lake, with an average N level of 1.58% as opposed to 1.06% for Binatang, mat thickness may have been offset by greater availability of nutrients.

The ideal situation for the Sepik region would be destruction of weed mats in open water, leaving a residual *C. salviniae* population in a thin fringe of salvinia growing among marginal vegetation. Imbuando Lagoon is now at this stage and others are approaching it. Lagoons which have very heavy sudd cover may require initial treatment with herbicide. Regrowth would then consist of small, mobile mats, relatively rich in nutrients released from decaying, sprayed plants, and would provide ideal conditions for *C. salviniae*.

Until now, the major problem with salvinia management has been the need for costly, repetitive spraying to deal with regrowth from the few inevitable survivors of a herbicidal control programme. *C. salviniae* appears to have the potential to be the major component of integrated programmes for management of both established, previously intractable, salvinia infestations and new infestations at greatly reduced cost.

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Disclaimer

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Chapter Seven
Biological Control of Weeds with Pathogens

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Host Specificity of Plant Pathogens in Biological Weed Control

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Abstract

Host specificity is a major concern in biological weed control programs. Exhaustive studies are conducted to ensure that the biocontrol agent, if released, will not damage desirable plants. The value of some tests used to determine the host range of candidate agents has been questioned and perhaps many potentially valuable biocontrol agents have not been released due to aberrant feeding on non-host plants in those tests. Host range studies with plant pathogens in controlled environment conditions have often resulted in broader host ranges than reported or previously known. The host ranges of *Puccinia* species being considered for introduction into North America have been artificially expanded within controlled environment containment facilities. Perhaps these expanded host ranges should have been expected, however, additional tests must be developed to evaluate actual or field specificity. Concerns for host specificity are not limited to classical biocontrol candidates since facultative saprophytes are being evaluated as biological herbicides. These pathogens tend to have broader host ranges than obligate parasites, but variation in laboratory and field specificity are also to be expected. Strict host specialization is not a requirement for biological herbicides.

La Spécificité des Phytophatogènes en Lutte Biologique Contre les Plantes Nuisibles

La spécificité des organismes utilisés en lutte biologique est une préoccupation constante chez les chercheurs. Ils doivent mener des études approfondies afin de s'assurer que l'organisme, une fois libéré, n'endommagera que les plantes cibles. La valeur de certains tests utilisés pour déterminer les hôtes potentiels d'agents de lutte biologique est discutable; il se peut que dans certains cas, des agents de lutte prometteurs n'ont pas été libérés dû au fait qu'ils démontraient des comportements anormaux d'alimentation sur certains hôtes reconnus comme non-susceptibles à leurs attaques. Des tests de spécificité d'hôtes avec des phytophathogènes, menés en laboratoire sous conditions atmosphériques contrôllées, ont revélé un nombre plus élevé d'hôtes potentiels que ce qu'avait été décrit ou était connu jusqu'à présent. La liste d'hôtes potentiels de certaines espèces de *Puccinia*, présentement évaluées pour leur introduction en Amérique du Nord, a ainsi été élargie de facon artificielle du fait que ces tests ont été menés sous les conditions closes d'un phytotron. Quoique ces résultats auraient dû être prévisibles, il n'en demeure que des tests additionels devront être développés afin d'évaluer la spécificité du phytopathogène telle qu'elle se manifeste en milieu naturel. Ces inquiétudes vis-à-vis la spécificité ne sont pas limitées aux candidats de l'approche classique de lutte biologique car certains saprophytes facultatifs sont évalués comme herbicide biologique. Ces phytopathogènes tendent à avoir une gamme d'hôtes plus considérable que dans le cas des parasites obligatoires. Neanmoins il faut prévoir des variations au niveau de leur spécificité tant en laboratoire qu'aux champs. Les herbicides biologiques ne requièrent pas une spécificité stricte du phytopathogène.

Introduction

Biological weed control is the deliberate use of natural enemies to reduce the population of a target weed. The classical and the inundative methods are the two main approaches, with classical biological control directed towards controlling naturalized weeds through the introduction of exotic natural enemies from the weed's native range and inundative biological control directed towards mass production and release of endemic natural enemies. Plant pathogens are being used in both classical and inundative biological weed control programs, and as suggested by many authors (Hasan 1983; Leonard 1982; Quimby and Walker 1982; Schroeder 1983; Templeton and Smith 1977; Wapshere 1982, 1983), host plant specificity is the most important factor in the selection of candidate pathogens as biocontrol agents.

Specificity in Plant Pathogens

The host range of plant pathogens may be narrow or broad, but most plant pathogens, whether facultative saprophytes or obligate parasites, generally have host ranges limited to one or a few species (Gäumann 1950; Holcomb 1982; Johnson 1976; Oku *et al.* 1979). Brian (1976) described the levels of specificity of fungal pathogens from non-pathogens to formae speciales and concluded that most fungal pathogens show a high degree of host specificity. However, little is known of the chemical basis of such specificity in pathogens (Oku *et al.* 1979).

Considerable variation occurs in the reported specificity of some pathogens (Brian 1976; Cother 1975; Eshed and Dinoor 1981). Often the procedures used to determine the host range and/or the taxonomy of the pathogen involved have been suggested as reasons for these discrepancies in the literature (Brian 1976; Eshed and Dinoor 1981). Another factor which compounds the difficulties in delimiting host ranges is the confusion concerning many terms used by various authors to discuss plant pathogen specificity. Merrill (1980) describes the major problem of concepts and terminology of such terms as resistant, susceptible, and immune. These terms, and others, have different usage from one report to another and consequently results of host specificity determinations can have many interpretations. A portion of Merrill's (1980) glossary is presented in Table 1 and it is suggested that this terminology be the basis of host specificity determination in biological weed control using plant pathogens.

As described earlier, specificity is a major concern in biological weed control and it is the responsibility of the biological control researcher to determine the host range of the candidate biocontrol agent. In plant pathology, disease or the host-parasite interaction is the product of the interaction between pathogen and a host in a given environment. These three factors (the pathogen, the host and the environment) must be considered in the development of appropriate or realistic host specificity testing procedures.

Host Specificity Testing

Because of the importance of safety in biological weed control programs, much has been written on host specificity screening and the limitations of these tests (Dunn 1978; Harris and Zwölfer 1968; Schroeder 1983; Wapshere 1974, 1982, 1983; Zwölfer and Harris 1971). Presently, most host specificity testing follows the centrifugal phylogenetic method proposed by Wapshere (1974) which delimits the extent of the biocontrol agent's host range and includes the testing of other plant species 'at risk'. Plants species 'at risk' tested should include those: (1) related to the target weed; (2) not previously exposed to the biocontrol agent; (3) having limited information on their natural enemies; (4) having similar secondary compounds and/or morphological similarities with the target weed; (5) attacked by related organisms; and (6) recorded as hosts of the candidate agent (Schroeder 1983; Wapshere 1982, 1983).

I concur with Schroeder's (1983) statement: 'Simple infectivity tests are made with pathogens ... phytophagous insects require more elaborate tests', but his conclusion, 'A

Table 1. Glossary of selected terms related to plant pathogen specificity (from Merrill 1980).

AGGRESSIVENESS:	The rate at which virulence is expressed; i.e., if two organisms produce equal-sized lesions on a host, but one does it in 2 days whereas the other requires 4 days, the first is more aggressive (twice as aggressive) than the second.
ESCAPE:	An inherently susceptible plant that does not become infected in the field due to chance, some quirk of nature, some property of the suscept itself other than resistance (*q.v.*), or because environmental conditions were not suitable for infection.
FIELD RESISTANCE:	The inherent ability of a plant to reduce the amount of rate of disease development caused by all races of the pathogen. The term is synonymous with horizontal resistance, nonspecific resistance, etc.
HYPERSENSITIVITY:	Extreme sensitivity to the pathogen, so that there is death of host cells and temporary or permanent inactivation of the pathogen at the point of attack, thus limiting infection.
IMMUNE:	Exempt from infection.
PATHOGENIC:	Able to cause disease.
PATHOGENICITY:	The capability of being pathogenic.
PREDISPOSITION:	The weakening of an organism by some factor(s) of either the physical or biotic environment so as to render the organism more susceptible to a pathogen.
RESISTANCE:	The inherent ability of an organism to overcome in any degree the effects of a pathogen. It implies that the pathogen is able to infect the organism, and thus to react with it. If no such reaction occurs, then the organism is not resistant but immune (*q.v.*). Thus immunity is not the highest form of resistance, but is distinct from it. Two types of resistance have been denoted: major gene resistance = vertical resistance = specific resistance = oligogenic resistance = resistance controlled by one or a few genes, and operative against only certain races of the pathogen. In contrast, minor gene resistance = nonspecific resistance = field resistance = polygenic resistance = horizontal resistance = resistance controlled by a few to several genes, each perhaps acting in an additive manner, and effective to some extent against all races of the pathogen.
SUSCEPT:	An organism that can be attacked by, or is non-immune to, a given pathogen.
TOLERANCE:	The capacity of a plant to endure disease; i.e., the inherent ability to become severely diseased without significant reduction in *yield* . Severity of symptom expression is disproportionately greater than reduction in yield.
VIRULENCE:	A measure of the degree of pathogenicity (*q.v.*)

pathogen is considered a safe biological control agent if it is unable to develop and produce disease symptoms on any of the test plants' requires further comment.

It has been suggested by Hasan (1983), Schroeder (1983), and Templeton and Trujillo (1981) that host specificity tests using plant pathogens should be conducted under controlled conditions that are optimum for infection and disease development on the target weed. Unfortunately, results of host range or pathogenicity tests obtained from laboratory, growth chamber and greenhouse studies bear little, if any, similarity to what may occur in the field (Colhoun 1973, 1979; Cother 1975; Johnson and Taylor 1976; Yarwood 1959). Under artificial growth conditions the host ranges of many facultative saprophytes and obligate parasites have been artificially expanded (Table 2). There have been many cases of successful artificial inoculations of plants with pathogens which are not associated with these plants in the field.

Table 2. Some examples of pathogens which have had their field host range expanded in greenhouse or growth chamber conditions.

Pathogen	Reference
Alternaria cassiae Jurair & Khan	Walker (1982)
Cercospora rodmanii Conway	Conway & Freeman (1977)
Erysiphe graminis DC.	Colhoun (1979)
Fusarium lateritium (Nees) emend. Snyder & Hansen	Walker (1981)
Phakopsora pachyrhizi Syd.	Bromfield & Hartwig (1980)
Phytopthora infestans (Mont.) de Barry	Müller (1950)
Phytopthora palmivora (Butl.) Butl.	Ridings *et al.* (1978)
Puccinia carduorum Jacky	Politis *et al.* (1984)
P. jaceae Otth	Watson & Alkhoury (1981); Mortenson (1985)
Puccinia centaureae DC.	Clément & Watson (1985)
Rhynchosporium secalis (Oud.) Davis	Ali (1974); Ali & Boyd (1974)
Septoria avenae Frank	Clark & Zillinsky (1960)

The concept of predisposition (the tendency of nongenetic condition, acting before infection to affect the susceptibility of plants) and the results of studies on predisposition (Colhoun 1973, 1979; Schoeneweiss 1975; Yarwood 1959) can be used to explain the greenhouse phenomenon or growth chamber phenomenon that we have been encountering in the host specificity determination of candidate plant pathogens. Many factors are implicated in the phenomenon of induced susceptibility with reduced light intensity, increased temperature and water stress known to increase the susceptibility of plants to disease (Colhoun 1973, 1979; Schoeneweiss 1975; Yarwood 1959). Heat-induced susceptibility to nonpathogens is usually associated with a short exposure of a high temperature (50°C) (Chamberlain 1972). However, results of Baker and Larter (1963) demonstrated that a temperature of only 25°C was sufficient to disrupt the effectiveness of resistant genes in two barley cultivars to *Rhynchosporium secalis* (Oud.) Davis (Hyphomycetes). Environmental factors do affect the cuticle of plants (Schoeneweiss 1975) and secretions from the cuticle (Schönbeck 1976) which can affect infection by many plant pathogens.

It is obvious that environment has a profound effect on plant pathogen specificity and it appears relatively easy to expand the field host range of a plant pathogen (a candidate biocontrol agent) whether a facultative saprophyte or an obligate parasite, by testing in artificial greenhouse or growth chamber conditions. Therefore, in addition to the need for more realistic inoculation or testing procedures (Cother 1975), we must be cautious in the interpretation of results obtained in our host specificity tests.

Interpretation of Results

The problem in accounting for the aberrant feeding of candidate biocontrol insects has received much attention in terms of host specificity testing procedures and conflict of interest discussions. The problems associated with interpretation of host range studies of plant pathogens conducted in greenhouses and controlled environment cabinets are probably more acute. Results of host range studies are questionable if the inoculation techniques and growth parameters are widely divergent from what naturally occurs in the field (Cother 1975). Interpretation of results obtained from inoculations under artificial conditions must be cautious and based on a sound, uniform understanding and interpretation of resistance and susceptibility in plant pathology.

Resistance and susceptibility are not absolute, but are different ends of the same scale (Gäumann 1950; Gracen 1982; Kuć 1979; Merrill 1980; Schoeneweiss 1975; Yarwood 1959). Plants which are not infected are not resistant, and should be termed immune. Resistance is thought to result from a specific interaction between the host and the pathogen, whereas susceptibility implies an absence of such an interaction (Johnson 1976). Daly (1976) suggested that 'induced susceptibility' observed in artificial growth conditions was an impairment of the host's capacity to respond to signals of the infection. This suggests that resistance is an active process which represses or inhibits the invading microorganism.

The interpretation of susceptibility data is also often confounded by the absence of quantitative data. Results of host range studies with plant pathogens for biocontrol are presented in different ways from the infection type scale (0–4) for rust pathogens (Hasan 1972; Politis *et al.* 1984), disease ratings scale (0–5) (Walker and Sciumbato 1981) to a simple disease reaction with S = susceptible and R = resistant (Walker 1981, 1982).

It is not my intention to suggest the most appropriate rating system for our biocontrol studies since each case is different and one scale may be more appropriate depending on the characteristics of the host-pathogen and the response range. However, it is imperative that we recognize the importance of using standardized terminology and that we use disease rating systems that are as descriptive as possible. For example, Daniel *et al.*'s (1973) use of the term tolerant in their Table 2 should have been replaced by resistant or perhaps immune.

Results of host range studies obtained in artificial growth conditions give an indication of what may happen in the field, but these results do not provide indisputable evidence as to the susceptibility of a plant to a certain pathogen (Cother 1975). Possible explanations for the extended or broader host ranges of pathogens tested under growth chamber and greenhouse conditions are: (1) the pathogen and host have not come into effective contact in nature; (2) field observations have not been sufficiently intense; or (3) the results are artifacts of our testing program.

Specificity and Classical Biological Control

In classical biological control, it is difficult to overemphasize the importance of specificity. Rigorous host range testing is essential to ensure that a prospective exotic pathogen will not damage beneficial plants in the area or country of proposed introduction (Hasan 1983; Leonard 1982; Wapshere 1982). Early work with the heteroecious *Rumex* rust, *Uromyces rumicis* (Schum.) Wint. (Uredinales), found all test plants, except *Rumex crispus* L. and *R. maritimus* L. (Polygonaceae), were immune to infection with urediniospores (Inman 1971). However, Inman (1971) was unable to infect the known alternate host, *Ranunculus ficaria* L. (Ranunculaceae), with teliospores and the host range of this spore stage could not be tested. Absence of host range data on the teliospore stage prevented possible consideration for introduction of *U. rumicis* into North America. Recent work in Switzerland has produced techniques for obtaining teliospore germination and infection of the alternate host, thereby enabling the host range tests to be completed (Schubiger *et al.* 1985). Both spore stages of this rust appear to be narrowly restricted in their host range.

Elaborate host range tests with the autoecious rust *Puccinia chondrillina* Bubak & Syd. (Uredinales), confirmed its strict specialization to one host plant, *Chondrilla juncea* L. (Compositae) (Hasan 1972). Specificity in this pathogen is so strict that certain strains are virulent on only one form of *C. juncea*. The original virulent strain imported from Vieste, Italy, into Australia for the common form of *C. juncea* was capable of infecting the other two Australian forms, although less vigorously. However, after prolonged rearing and introduction into Australia it was unable to infect the other two forms (Cullen 1974).

The interpretation of the host range results of the strictly specialized *P. chondrillina* was relatively straightforward and the success of the *Chondrilla* rust program provided encouragement for research on rust pathogens of *Carduus*, *Centaurea* (both Compositae) and other weedy genera. Autoecious rusts of *Carduus* and *Centaurea* are reported to have narrowly restricted host ranges (Gäumann 1959; Guyot 1967; Ialongo and Boldt 1977; Savile 1970*a*, *b*, 1973). Host range testing of some of these *Puccinia* species have been conducted in containment facilities in the United States and in Canada. In all studies conducted to date, the laboratory (greenhouse or growth chamber) host range is broader than the reported field host range of these rusts. The controlled environment host range of *P. jaceae* Otth. includes safflower (*Carthamus tinctorius* L.; Compositae) (Mortensen 1985; Watson and Alkhoury 1981); *P. centaurea* DC. includes safflower (Clément and Watson 1985), and *P. carduorum* Jacq. includes globe artichoke (*Cynara scolymus* L.; Compositae) (Politis *et al.* 1984). These crop plants have not previously been reported as hosts of these rusts. Details of these host range studies are published elsewhere or are in preparation. It is of interest to note that *P. carduorum* is already present in North America (Watson and Brunetti 1984), as is *P. centaureae* (Savile 1970*b*) and perhaps so is *P. jaceae*. Interpretation of these results for the *Carduus* and *Centaurea* rusts are difficult and further studies are required before valid decisions on whether or not to introduce them can be made.

Specificity and Biological Herbicides

Since native plant pathogens are being evaluated as biological herbicides, strict host specialization is not required. Some authors have indicated that bioherbicide pathogens must be host specific (Auld *et al.* 1983; Hasan 1983). However, most fungi that are being evaluated as potential bioherbicides are facultative saprophytes with relatively wide host ranges, including some host-limited strains (restricted to one or a few plant species) (Daniel *et al.* 1973; Ridings *et al.* 1978; Walker 1981, 1982). Wapshere (1982) used the phrase 'sufficiently safe' which aptly describes the host specificity requirements of bioherbicides.

One of the first organisms to be evaluated as a biological herbicide, *Colletotrichum gloeosporioides* (Penz.) Sacc. f. sp. *aeschynomene* (Melanconiales), was thought to be narrowly specialized (Daniel *et al.* 1973), but recent tests involving more species has revealed a larger host range than originally described (TeBeest 1984). Greenhouse and growth chamber host range studies with other native facultative saprophytes considered for the bioherbicide approach have not demonstrated strict host specialization (Conway and Freeman 1977; Ridings *et al.* 1978; Walker 1981, 1982; Walker and Sciumbato 1979). When tested in field conditions, the host range is usually more restricted (Conway and Freeman 1977; Walker 1982).

In some respects, the host range evaluations of candidate bioherbicides are analagous to crop safety and efficacy testing for chemical herbicides. Obviously there must be a margin of safety required for crops in which the target weed occurs and this safety margin is less important for crops in which the target weed is not a problem. For example, atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-*s*-triazine] provides effective weed control in corn, but is not recommended for use in cereal crops because of its phytotoxicity to these crops.

Potential Risks and Suggested Approaches

No technology is without risk and the use of plant pathogens as biological control agents of weeds is no exception. As discussed in this paper, the major concern of biological weed control with plant pathogens is host specificity and the possible risk of damage to desirable plant species. Leonard (1982) has reviewed the hazards involved and suggested approaches to reduce these risks.

Host range changes could occur through mutation, adaptation, or hybridization or result from predisposition of the pathogen during host range studies. The number of mutations is a function of the number of spores produced. However, all mutations would not result in host range expansion, most mutations would be deleterious to the pathogen and some mutations may even be beneficial to the biocontrol program. The genetics of host specificity in most plant pathogens is complex and a single mutation is not sufficient to extend the host range of rust fungi (Leonard 1982). Is it reasonable to assume mutations occurring with a pathogen used in a biological weed control program to be different from those occurring or which have already occurred in the natural habitat?

Adaptation of a pathogen to become more virulent on a host plant is possible and has been demonstrated by repeated inoculation of some facultative saprophytes (Gäumann 1950; Johnson 1976; Leonard 1982). However, repeated passage through resistant or noncongenial host, especially for an obligate pathogen, reduces virulence and results in progressive reduction in inoculum quantity until the 'inoculum threshold' is reached, whereby there is insufficient inoculum for infection to occur (Gäumann 1950).

The possibility of hybridization occurring between two pathogens does exist, but as Leonard (1982) stated, inheritance at the host species level is very complex and hybrids usually have much reduced virulence on one or both parents. The prospects of virulent, aggressive hybrids developing from crosses between *P. jaceae* and *P. carthami* Corda or *P. centaureae* and *P. carthami* are remote. However, these crosses should be attempted within containment facilities.

Although predisposition is not associated with an actual change or alteration in the pathogen, it does have an effect on the expression of host range. Host range testing in controlled environment conditions tends to predispose plants to infection which results in artificial expansion of the host range. The possibility of predisposing normally susceptible plants to become resistant in these tests is less likely (Colhoun 1973, 1979; Yarwood 1959).

Concerns of risk and conflicts of interest with the use of plant pathogens as biocontrol agents for weeds will likely intensify. Questions of host specificity testing methods and data interpretation have been discussed and the potential for use of plant pathogens in biological weed control programs remains outstanding. Host range studies conducted solely in controlled environment conditions are not adequate for accurate host range determination of candidate biocontrol pathogens. I support the suggestions of Conway and Freeman (1977), Cother (1975), and others and strongly recommend: (1) Host range studies be conducted under realistic conditions that closely approximate the natural situation of the plant, the pathogen and the environment; and (2) Host range testing be two-phased with the first phase conducted within controlled environment conditions followed by a second phase of field evaluation. The field studies should be appropriately designed and replicated trials which are repeated each growing season for at least two or more (preferably three) growing seasons. Field evaluation of native pathogens requires fewer precautions and depending on the level of risk, exotic pathogen field testing may be restricted initially to the country of origin.

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Damage to *Senecio jacobaea* by the Rust Fungus *Puccinia expansa*

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Abstract

Plants of *Senecio jacobaea* (ragwort) were repeatedly infected by the rust fungus *Puccinia expansa* in greenhouse experiments. Dry weight of rusted plants, harvested approximately 80 days after seed, was 50% less than that of healthy plants. Reduction of number of assimilating leaves was about 46%. Dry weight of rusted plants, harvested approximately 110 days after seed, was 62% less than that of healthy plants. Reduction of number of flowers/plant was about 42%. The rust had no significant influence on initiation of stem elongation. These results show that *P. expansa* could be of value in biocontrol of *S. jacobaea*, especially in combination with the insects *Tyria jacobaeae* and *Longitarsus jacobaeae*.

Dommage causé au *Senecio jacobaea* par la rouille *Puccinia expansa*

Dans des expériences en serres, des plantes de *Senecio jacobaea* ont été infectées de façon répétée avec la rouille *Puccinia expansa*. Le poids à sec des plantes rouillées, moissonées 80 jours environ après la montée en graine, n'atteignait que 50% de celui des plantes saines. La réduction du nombre de feuilles assimilantes était de 46% environ. Le poids à sec des plantes rouillées, moissonées 110 jours environ après la montée en graine, était 62% moins élevé que celui des saines. La réduction du nombre de fleurs d'une plante infectée était de 42% environ. La rouille ne pas influencé, de façon significative, l'initiation de la croissance des tiges. Ces résultats indiquent que le *P. expansa* pourrait être utile dans la lutte contre le *S. jacobaea*, surtout en combinaison avec les insects *Tyria jacobaea* et *Longitarsus jacobaeae*.

Introduction

Senecio jacobaea L. (ragwort; Compositae) is a serious weed on pastures in many parts of the world. According to Schmidl (1972*a*) in Victoria (Australia) more than half a million dollars (Australian) are spent annually on control of ragwort; in Oregon the minimum economic loss/year is estimated about 1.5 million U.S. dollars (Isaacson 1978). *S. jacobaea* spreads rapidly and decreases production of pastures. Moreover it contains pyrrolizidine alkaloids, which are toxic to cattle and horses. The plant is often present at various growth stages at the same time (as seedlings, rosettes of various ages, in full flower or in seeding stage). This makes chemical control often unreliable (Harper and Wood 1957; Schmidl 1972*a*). Therefore biological methods for control of ragwort, such as introducing exotic insects, have been investigated by different laboratories (Schmidl 1972*b*; Cullen and Moore 1981).

The lepto-rust *Puccinia expansa* Link (= *P. glomerata* Grev.) (Uredinales) attacks and deforms leaves and flowering stems of *S. jacobaea*. In greenhouse experiments two strains of the rust, collected on *S. alpinus* L. in Switzerland, did not infect any beneficial plants outside the genus *Senecio*. Therefore *P. expansa* could be considered specific enough to be a biological control agent against *Senecio* weeds (Alber *et al.* 1984).

The object of this study was to determine the influence of *P. expansa* on growth of *S. jacobaea* under greenhouse conditions; in particular, effect on number of leaves and flowers, and on dry weight of plants.

Materials and Methods

Plant Material

Seeds of *S. jacobaea* were collected at Sonnenberg (800 m), near Lucerne, Switzerland in 1981.

Rust Material

Teliospores of *P. expansa* (strain Se-9) were collected on *S. alpinus* in Justistal (1200 m), Switzerland, in 1982. Since then the strain was maintained and propagated in the greenhouse.

Table 1. Time table of inoculations and harvests of plants in the experiments I and II.

	Days after seed		Quantity of spore suspension, 10^5 spores/ml
	I	II	I and II
1. Inoculation	35	40	150 ml
2. "	49	54	150 ml
3. "	63	68	200 ml
First harvest of plants	77	78	–
4. Inoculation	77	78	200 ml
5. "	91	88	200 ml
6. "	105	98	200 ml
Second harvest of plants	119	108	–

Methods

Plants were grown from seeds and individually potted in clay pots (height 14 cm, diam. 12 cm) in sterilized soil (Potgrond Topferde, De Baat, Netherlands) mixed with Perlit (PePe, granular mineral of quartz expanded by heating) in proportion 5:1. For experiments, plants were divided into two groups of 30 plants (15 control, 15 treatment) and maintained in separate greenhouse chambers under the same conditions (8 h dark at 15°C and 16 h light at 20°C; 80% r.h.). Once a week plants were fertilized with 125 ml/plant of 0.1% Lonzin (16% N, 16% P_2O_5, 16% K_2O and trace elements).

Plants in treatment groups were inoculated three or six times with *P. expansa* in intervals of 14 and 10 days respectively (Table 1). Inoculation occurred by regularly spraying a teliospore suspension (150 or 200 ml; see Table 1) of 10^5 spores/ml tap water containing 0.05% Etalfix (adhesive Maag AG, Switzerland). Teliospores were pretreated by storing for 21 days on water agar at 8°C (Alber *et al.* 1984). At the moment of each inoculation a germination test of the spore suspension on water agar was made.

Plants in control groups were sprayed with the same amount of tap water containing 0.05% Etalfix. After treatment, plants were incubated for 72 h under a plastic tent. Ten to fourteen days after the third inoculation, half of the plants of both groups were harvested (Table 1). Harvesting included cutting the plants 1 cm above the soil surface. The number of assimilating leaves was counted. Dry weight was determined after drying the plant material for 24 h at 105°C. Ten to fourteen days after the sixth inoculation the second harvest occurred by cutting the whole plants 1 cm above the soil surface (Table 1). Number of flowers (including buds, flowers and faded flowers) was counted, and dry weight of whole plants determined. Time of stem elongation was also assessed. The whole experiment was repeated on two different days (experiment I and II).

Statistical Analysis

Data from each harvest were analysed separately using Student's *t*-test. Statistical differences with a significance level of $P < 0.01$ are indicated with three stars (***), those with a significance level of $P < 0.10$ with one star (*) (Figs. 1–4). The difference between means of control and treatment expressed in percent of the mean of controls gives the reduction by the rust infection (Table 2).

Results

The average percent germination of teliospore suspensions was always 50–70%. In general, first infection symptoms (light-green spots) occurred 7–9 days after inoculation. Numerous pustules developed on leaves, leaf stems, flowering stems and peduncles 2–3 days later.

Damage to S. jacobaea *at First Harvest*

In both experiments *P. expansa* reduced dry weight of plants and the number of assimilating leaves significantly ($P < 0.01$). Mean dry weight of rusted plants was 50% of that of healthy plants (Table 2, Fig. 1). The reduction of number of leaves was by 46% (Table 2, Fig. 2).

Damage to S. jacobaea *at Second Harvest*

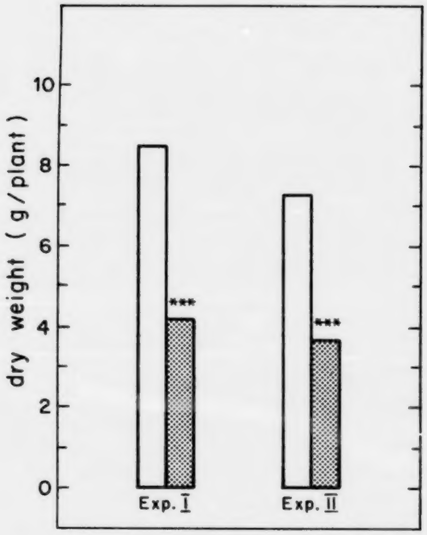
In both experiments the rust reduced dry weight of plants significantly ($P < 0.01$). Mean dry weight of rusted plants was 62% less than that of healthy plants (Table 2, Fig. 3). Reduction of flowers/plant was by 42%, but in experiment I only significant at $P < 0.10$ and in experiment II not significant (Table 2, Fig. 4).

Influence of the Rust on Stem Elongation of S. jacobaea

The rust had no significant influence on the beginning of stem elongation. In control and treatment groups, 74 days after seed (experiment II: 57 days) stem elongation was first observed.

Discussion

Basidiospores (produced by teliospores) of rust fungi need dew or raindrops to infect their host plants. Unfavourable moisture conditions and the absence of wind in the greenhouse prevented a reinfection of *S. jacobaea* by spontaneously germinating teliospores. For this reason plants were repeatedly inoculated to imitate favourable natural conditions.



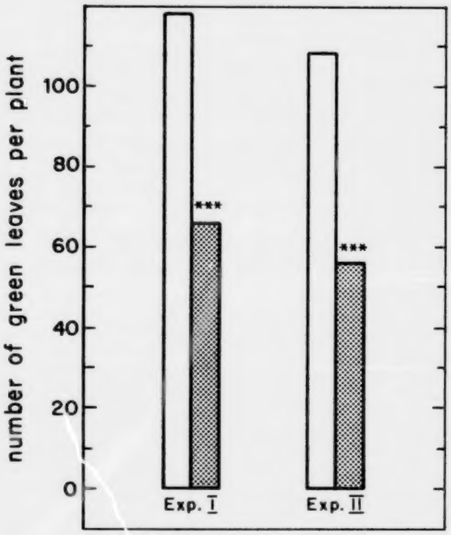
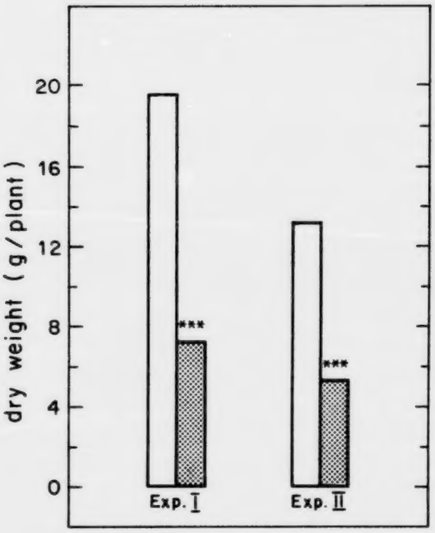


Fig. 1. (Left) Effect of *Puccinia expansa* Link on dry weight of *Senecio jacobaea* L.; plants harvested approximately 80 days after seed (first harvest). Means based on 15 plants. ***, significant at $P < 0.01$; *, significant at $P < 0.10$; n.s., not significant; ☐ control; ▨ treatment.

Fig. 2. (Right) Effect of *Puccinia expansa* Link on number of assimilating leaves of *Senecio jacobaea* L.; plants harvested approximately 80 days after seed (first harvest). Means based on 15 plants (see Fig. 1).



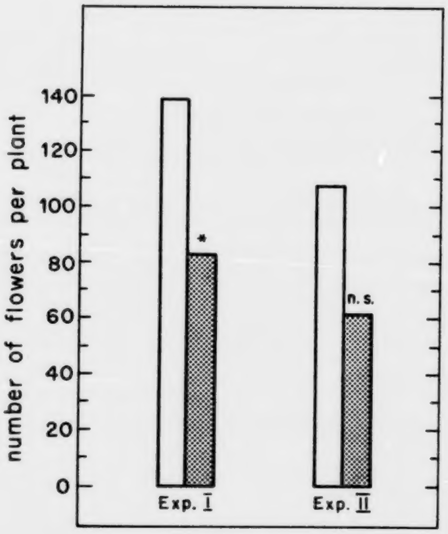


Fig. 3. (Left) Effect of *Puccinia expansa* Link on dry weight of *Senecio jacobaea* L.; plants harvested approximately 110 days after seed (second harvest). Means based on 15 plants (see Fig. 1).

Fig. 4. (Right) Effect of *Puccinia expansa* Link on number of flowers/plant (*Senecio jacobaea* L.); plants harvested approximately 110 days after seed (second harvest). Means based on 15 plants (see Fig. 1).

S. jacobaea is normally a biennial plant (Harper and Wood 1957). Therefore, in the greenhouse not all plants had formed flowering stems and flowers by the second harvest, resulting in several values of zero. For this reason the standard deviation of the values was too high, and thus reduction of number of flowers/plant not statistically significant.

Loss of dry weight described in this paper is similar to that observed by other authors working with fungal pathogens or insects. Hasan (1974) showed that in field experiments the rust fungus *Puccinia xanthii* Schw. reduced dry weight of *Xanthium strumarium* L. (Compositae) by 37%. Schmidl (1972*b*) found that in field experiments the cinnabar moth *Tyria jacobaeae* L. (= *Callimorpha jacobaeae* L.) (Lepidoptera: Arctiidae) reduced dry weight of *S. jacobaea* by 58%, and number of flowers by 64%. *T. jacobaeae* has already been successfully used as a biocontrol agent in Oregon (Isaacson 1978).

Table 2. Reduction of dry weight, number of green leaves and flowers/plant of *Senecio jacobaea* L. due to infection by *Puccinia expansa* Link, expressed in percent of healthy plants. Means based on 15 plants.

	Harvest 1: 80 days after seed			**Harvest 2: 110 days after seed**		
	Experiment					
	I	II	*	I	II	*
Dry weight (g)	49.8%	49.9%	50%	63.1%	60.5%	62%
No. of green leaves/plant	43.9%	48.2%	46%	_	_	_
No. flowers/plant	_	_	_	40.7%	43.3%	42%

* Average of both experiments.

According to Schmidl (1981), successful biological control of a weed usually requires a number of interacting organisms. Besides *P. expansa*, he also mentions the insects *T. jacobaeae* and *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae) for ragwort control.

The results of this paper show that *P. expansa* has good control potential in the greenhouse, but further experiments under field conditions are necessary.

Acknowledgments

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Biological Control of *Carduus pycnocephalus* with *Alternaria* sp.

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Abstract

An *Alternaria* sp. resembling *Alternaria zinniae* was isolated from Italian thistle (*Carduus pycnocephalus*) and evaluated for possible use as a biological control agent. Typical symptoms include small, dark brown to black, target spot lesions on cotyledons and foliage leaves that can coalesce and stunt or kill the plant. Cotyledons were more susceptible to the fungus than later stages of growth, showing a greater percent of lesion area at a given inoculum concentration. Dew periods of at least 4 h at 13°C were required for establishment of infection. Severity of infection as measured by number of plants killed and percent of leaf area with lesions, increased rapidly with duration of dew periods to 16–24 h when inoculated with 2×10^5 conidia/ml. Decreasing temperature during inoculation in a moist chamber for 24 h from 20° to 5°C decreased disease severity significantly for all inoculum concentrations up to 10^6 conidia/ml.

An increase in inoculum concentration was related to an increase in percent of diseased leaf area at all temperatures investigated. An extensive host range study indicated that the fungus was pathogenic only on Italian thistle and slender thistle (*C. tenuifloris*).

Lutte Biologique contre *Carduus pycnocephalus* au Moyen de *Alternaria* sp.

Une *Alternaria* sp., similaire à *Alternaria zinniae*, a été isolée sur le chardon *Carduus pycnocephalus* et étudiée comme agent possible de lutte biologique. Les symptômes typiques du champignon sont de petites lésions allant du brun foncé au noir sur les cotylédons et les tissue foliaires qui peuvent se fondre ensemble et arrêter la croissance ou tuer la plante. Les cotylédons étaient plus vulnérables au champignon que les feuilles primaires et secondaires, et présentaient des lésions plus vastes à une concentration d'inoculum donnée. De jeunes plants âgés de 2 à 5 semaines ont été inoculés avec des doses de 0 à 10^7 spores de *Alternaria* sp. au millilitre et placés dans une chambre humide pendant 24 heures. L'augmentation de la concentration de l'inoculum a provoqué l'accroissement de la surface atteinte des feuilles. À une dose de 5×10^5 spores au millilitre, 90 à 100% de tous les tissus foliaires de 2 semaines mettaient en évidence des nécroses, tandis qu'il fallait une dose de 10^6 spores au millilitre pour provoquer le même effet chez les jeunes plants âgés de 5 semaines. Il fallait un minimum de 4 à 8 heures d'exposition à une humidité libre à 10°C pour que s'installe l'infection de *A. zinniae*. D'après une étude de spécificité d'hôtes, le champignon ne perturbe pas plusieurs cultures de la même famille que *Carduus* ou d'autres espéces de chardon.

Introduction

Italian thistle (*Carduus pycnocephalus* L.; Compositae) is an annual weed which was introduced to California in the 19th century from the southern Mediterranean region. This thistle is an important economic pest of pasture, rangeland and ruderal areas of coastal and central California (Dunn 1976). Seedlings emerge from late fall to early winter, often in thick stands. Temperatures from late November through March average 13°C in the day and 8°C at night in these areas and rainfall is usually sufficient to promote seed germination (Evans *et al.* 1979). At present the only reported disease on

C. pycnocephalus is *Puccinia cardui-pycnocephali* Syd. (Uredinales) (Gäumann 1959; Batra *et al.* 1981; Olivieri 1984). [The importance of this weed has prompted other studies of both fungi and phytophagous insects for the control of this and other *Carduus* species (Batra *et al.* 1981; Olivieri 1984; Surles and Kok 1978; Puttler *et al.* 1978).]

In winter 1982, a leafspot was observed in roadside stands of Italian thistle near Berkeley, California. Disease symptoms included dark, sharply delimited lesions, ranging in size from pin-point (< 1 mm diam.) to > 1 cm in diam. These lesions sometimes coalesced and killed the plant when weather conditions permitted. An *Alternaria* (Hyphomycetes) was consistently isolated from these lesions. No record of an *Alternaria* species infecting any *Carduus* species has been found for the United States or Europe. However, many *Alternaria* species have been successfully used to control other weed species (Walker 1981; Krupinsky and Lorenz 1983).

The objectives of these studies were to determine whether an *Alternaria* sp. isolated from *C. pycnoceophalus* was highly pathogenic to this species and whether other plants, including non-crop species, were susceptible to infection by this fungus. Also, the usefulness of this fungus as a biological control agent of *C. pycnocephalus* was examined by determining the optimum environmental conditions for infection, the effect of host phenology on infection and lesion development, and the quantitative infectivity of *Alternaria* sp. spores in relation to these other parameters. As this fungus had not been reported previously on *C. pycnocephalus*, an attempt was made to thoroughly describe its anatomical and biological characteristics to clarify its taxonomic position.

Materials and Methods

The isolate of *Alternaria* used in this study was obtained from diseased *C. pycnocephalus* cotyledons collected near Berkeley, California, in December 1983. Spores of this fungus were produced by a procedure similar to that of Walker and Riley (1982). Three-liter flasks containing 1 l of a culture medium consisting of soybean flour, 15 g/l; corn meal, 15 g/l; sucrose, 30 g/l; $CaCO_3$, 3 g/l; and distilled water were inoculated with a 1 cm^2 section of potato dextrose agar (PDA) containing mycelium of the fungus and inoculated for 3–4 days on a rotary shaker at 24°C. Mycelia were spearated from growth medium by filtration and minced for 30 sec in a Warring blender. The mycelial homogenate was poured into 40 × 60 cm plastic trays to a depth of *c.* 0.5 cm and incubated for 2 days at 24°C with an 11 h light-cycle as described by Walker (1980). The trays were allowed to air dry in a ventilated chamber for 24 h. The surface of the mycelial mat after drying was covered with conidiophores and conidia which were harvested with a cyclone spore collector (Tervet and Cherry 1950) and stored at 5°C until needed.

Plant Inoculation Studies

Seeds of *C. pycnocephalus* obtained from Mendocino and Alameda Counties in California were planted in 7 cm plastic pots containing UC soil mixture and were fertilized with half-strength Hoagland (Hoagland and Arnon 1950) solution. Plants were grown in a glasshouse at 16±2°C with natural lighting. Plants germinated after *c.* 4–7 days; the first true leaf appeared shortly after 2 wks. Plants were watered once a day at soil level after emergence to minimize wetting of the leaves. Seedlings of various stages of growth were inoculated with 100 ml of a spore suspension containing 0.03% Triton CS-7^R sticker-spreader in distilled water. Spore concentrations were estimated with a hemocytometer. Inoculum was sprayed onto plants using an atomizer, until runoff. Inoculated plants were placed in a light-proof moist chamber kept at 95–100%

r.h. by 2 DeVries cold air humidifiers. Unless otherwise stated, plants were kept in the moist chamber for 24 h at 13°C and then removed to a glasshouse. Symptoms were observed every day for 14 days.

The causal agents of the leaf spotting disease were identified by direct observation of sporulation on the surface of leaves placed in a petri dish lined with filter paper soaked in distilled water to achieve high humidity. Pathogenic fungi also were isolated after placing small, surface-sterilized leaf segments on PDA, and observing the presence of characteristic mycelia or spores produced by *Alternaria* sp.

Host Range Study

Other weeds and agronomic plants which grow in the same areas as *C. pycnocephalus* were inoculated with 10^6 spores/ml of *Alternaria* sp. as described above. Six plants in the cotyledon stage (one/pot) and six mature plants (one/pot) were inoculated. An equal number of uninoculated plants were used as controls. All plants in host range studies were examined for symptom development periodically for 28 days. Any necrotic tissue observed was plated on PDA or pea-straw agar to determine the presence of *Alternaria* sp.

Determinations of Environmental Effects on Infection

Eight groups of 10 cotyledon stage *C. pycnocephalus* plants were inoculated with 2×10^5 spores/ml *Alternaria* sp., and another group of 10 uninoculated plants were placed in a moist chamber at 13°C. One group of inoculated plants was removed from the moist chamber after either 0, 1, 4, 8, 12, 16, 24, or 30 h and was placed in a glasshouse to allow disease development. Plants were rated for disease incidence and percent of leaf area with lesions 2 wks after treatment using both visual assessment keys and a video assessment device as described previously (Lindow and Webb 1983; Lindow and Andersen 1984). This experiment was performed on two separate dates.

Groups of 20 plants in the cotyledon stage of growth were inoculated on two separate dates with spore suspensions containing either 0, 2×10^3, 1×10^4, 1×10^5, 1×10^6, or 5×10^6 spores/ml. The plants were placed in a moist chamber at 5°C for 24 h and then transferred to a glasshouse to allow disease development. Leaves were evaluated for area of necrotic lesions 7 and 14 days after inoculation. This experimental design was repeated at both 13 and 20°C.

Effect of Host Phenology on Infection

Ten *C. pycnocephalus* plants in the cotyledon, first leaf, second leaf, third leaf, and fourth leaf stage of growth were inoculated with 2×10^5 spores/ml and placed in a moist chamber for 24 h at 13°C with an equal number of uninoculated plants serving as controls. Each treatment was replicated twice. The plants were evaluated for disease incidence and percent of necrotic leaf area 2 wks after inoculation as described above.

Results and Discussion

Isolation and Cultural Characteristics of the Organism

Small, dark lesions were observed on emerging leaves shortly after emergence of *C. pycnocephalus* seedlings in the late fall of 1982 and 1983. The lesions occurred with a greater frequency in wet, shaded areas and were most prevalent several days after a rainfall, indicating that moisture is important for spread and/or development of the disease. The cotyledons of these plants were most frequently infected; only occasional lesions on more mature plants were observed. The leaves under a dense canopy of thistles had a greater incidence of the disease than did isolated plants.

Fungal spores typical of *Alternaria* were produced profusely on diseased leaf material placed in a plastic petri dish with high r.h. The conidia and conidiophores were observed directly from lesions or in culture on PDA or pea-straw agar. The fungus sporulated readily on pea-straw agar, producing septate, hyaline hyphae *c.* 7 μ wide. Aerial mycelium on pea-straw agar was cottony, 2–4 mm high, and white to pale gray. Sporulation occurred rarely on PDA. Aerial mycelium on PDA was cottony, 3–5 mm high, and off-white to pale gray.

On the basis of conidia morphology the fungus would be put in the noncatenate section of the genus *Alternaria* (Neergaard 1945). Conidia were formed singly on conidiophores. Secondary conidia appeared only rarely. An abrupt transition from spore body to beak was typical in conidia (Fig. 1). The spore body was 40–80 μ long, 15–25 μ wide, and had 4–10 transverse and 0–3 longitudinal septa. The spores are highly pigmented, ranging from brown to dark olive-brown. This fungus most resembles *A. zinniae* Pape based on morphological and cultural characteristics.

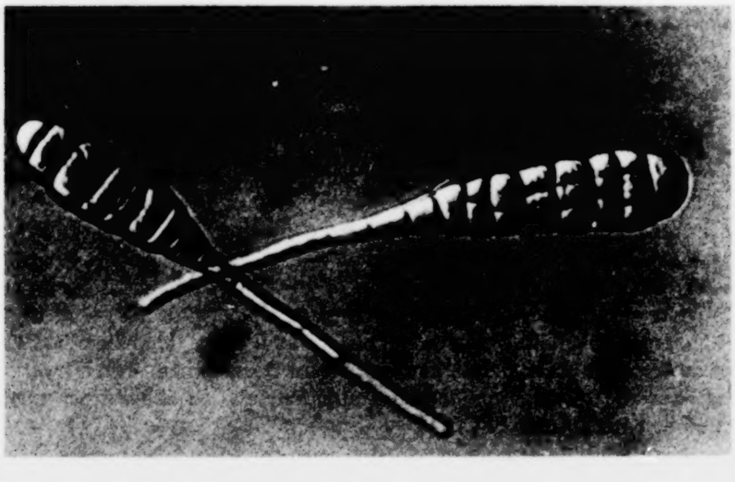

Fig. 1. Conidia of *Alternaria* sp. obtained from a sporulating lesion on a cotyledon of *Carduus pycnocephalus* L. (400 ×).

Pathogenicity Tests

All *C. pycnocephalus* plants in the cotyledon and third true leaf stage inoculated with the fungus developed lesions. The *Alternaria* sp. used in this study was consistently reisolated from necrotic lesions. None of the non-inoculated control plants developed lesions. The presence of infectious *Alternaria* sp. conidia isolated from the lesion tissue indicated that *Alternaria* sp. was the causal agent of the disease.

Host Range of Alternaria *sp.*

Lesion development occurred on *C. tenuifloris* Curt. and *C. pycnocephalus* plants inoculated with *Alternaria* sp. (Table 1). Plants in the cotyledon stage of growth were severely stunted or killed, while growth of infected mature plants was not affected significantly. *Alternaria* sp. was isolated in all cases from the lesion area. *Zinnia elangis* Jacq. (Compositae) plants at the cotyledon stage developed pin-point lesions following inoculation with 1 × 10^6 conidia/ml, but no *Alternaria* sp. was isolated from these areas. No other plant species developed any lesions after up to 28 days from inoculation.

Table 1. Susceptability of various plant species to *Alternaria* sp. in glasshouse.[1]

Species Tested	2 wks[2]	10 wks
Compostae		
Italian thistle (*Carduus pycnocephalus* L.)	+[3]	+
Slender thistle (*C. tenuafloris* Curt.)	+	+
Artichoke (*Cynara scolymus* L.)	–	–
Safflower (*Carthamus tinctorius* L.)	–	–
Milk thistle (*Silybum mariannum* [L.] Gaertn.)	–	–
Spiny sow thistle (*Sonchus asper* [L.] Hill)	–	–
Lettuce (*Latucca sativa* L.) var. "Greatlakes"	–	–
var. "Parris Island"	–	–
Zinnia (*Zinnia elegans* Jacq.)	±	–
Cucurbitaceae		
Cucumber (*Cucumis sativus* L.)	–	–
Gramineae		
Baryard grass (*Echinochloa crus-galli* [L.] Beauv.)	–	–
Johnson grass (*Sorghum halepense* [L.] Pers.)	–	–
Wild oats (*Avena fatua* L.)	–	–
Corn (*Zea mays* L.)	–	–
Leguminosae		
Kidney bean (*Phaseolus vulgaris* L.)	–	–
String bean (*Phaseolus vulgaris* L.)	–	–
Soybean (*Glycine max* [L.] Merr.)	–	–
Malvaceae		
Cotton (*Gossypium hirsutum* L.)	–	–
Solanaceae		
Potato (*Solanum tuberosum* L.)	–	–
Tomato (*Lycopersicon esculentum* Mill.)	–	–
Tobacco (*Nicotiana tabacum* L.)	–	–
Umbelliferae		
Carrot (*Daucus carota* L. sub. sp. *sativus* [Hoffm.] Arcang.)	–	–

[1] Plants inoculated with 1x10^6 conidia/ml. of *Alternaria* sp. Evaluations were made to 28 days after inoculation.

[2] Plants inoculated 2 wks and 10 wks after germination.

[3] (+) = lesion development from which *Alternaria* sp. was isolated; (–) = no symptoms observed; (±) = pinpoint lesions from which no *Alternaria* could be isolated.

A. zinniae has been reported as a pathogen of zinnia, lettuce and tomato (Neergaard 1945). This isolate of *A. zinniae* does not exhibit this host range. More detailed work is required to determine if this is a strain of *A. zinniae* with an attenuated host range or a previously undescribed species.

Host Phenology Effects on Infection

Susceptibility of *C. pycnocephalus* to *Alternaria* sp. decreased with increasing stage of plant growth (Table 2). The disease was lethal to plants only in the cotyledon and first leaf stage of growth. Average lesion area on infected leaves was examined to determine the relative severity of infections caused by the pathogen. The lesions did not expand beyond 1 cm^2 on the older leaf tissue and all new growth (exposed to inoculum) was free of infection. Since the plant can recover from even heavy infection if it is not killed, it will likely be important to establish high levels of infection by inoculation at the cotyledon stage for adequate control in the absence of other stresses to this weed.

Free Moisture Requirements

A minimum of 4 h in a water-saturated atmosphere was required for infection of the host plant at 13°C by *Alternaria* sp. (Fig. 2). The severity of infection and subsequent disease symptoms increased with increased free moisture periods for up to 24 h when all plants were killed when sufficient inoculum was applied. This indicates that while substantial numbers of infections could occur following short dew periods in clear nights conducive for radiative dew formation, dew periods are not sufficient for optimum infection under field conditions and must be supplemented by rainfall.

Table 2. Effect of stage of growth on plant mortality and percent of leaf area with lesions on *Carduus pycnocephalus* L. inoculated with *Alternaria* sp.[1]

Growth stage	Plants killed		% Lesion area	
	inoc.	control	inoc.	control
Cotyledon	100	0	100 ±0[2]	0
Cotyledon-1 leaf	85	0	92.1 ±6.3	0
1 - leaf	0	0	42.8 ±18.1	0
2 - leaf	0	0	19.5 ±5.6	0
3 - leaf	0	0	9.6±2.5	0
4 - leaf	0	0	11.9 ±5.0	0

[1] Twenty plants of each growth stage were inoculated with $2x10^5$ condidia/ml and incubated at 13° C with a 24 h dew period. Plants were evaluated 14 days after inoculation.

[2] Values of the standard error of a treatment mean at $P = 0.05$.

Interaction Between Inoculum Concentration and Temperature at Time of Inoculation

The severity of disease on *C. pycnocephalus* inoculated with *Alternaria* sp. was increased with increasing spore concentrations at all temperatures of inoculation (Fig. 3). When the temperature was reduced, however, the number of infections at any given inoculum concentration was also reduced. All plants in the cotyledon stage of growth were killed following an inoculation with 10^5 spores/ml at 20°C (100% lesion area) while equivalent numbers of plants were killed at 13 and 5°C only when 10^6 spores/ml and 5×10^6 spores/ml, respectively, were applied. It is important to determine in more detailed studies if temperature is a limiting factor for infection with *Alternaria* sp., because the most susceptible cotyledon stage of growth occurs in the early winter when minimum average yearly air temperatures occur.

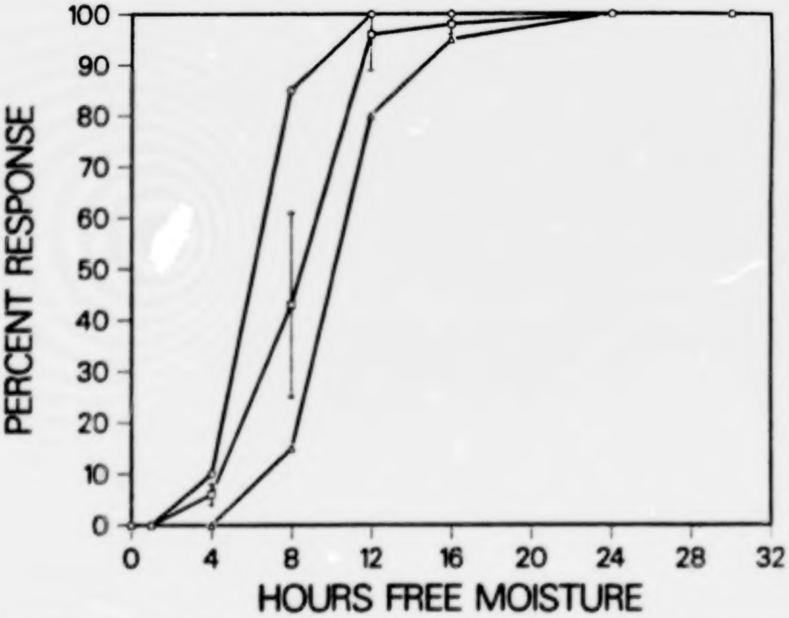

Fig. 2. Effect of free moisture on establishment of *Alternaria* sp. on *C. pycnocephalus* L. Plants were inoculated with 2 × 10^5 spores/ml and placed in moist chamber at 13°C for the times indicated on the abscissa. The incidence of disease (percent plants infected (○), the percent of plants killed (△), and the median percent of leaf necrosis (□) after 7 days is reported.

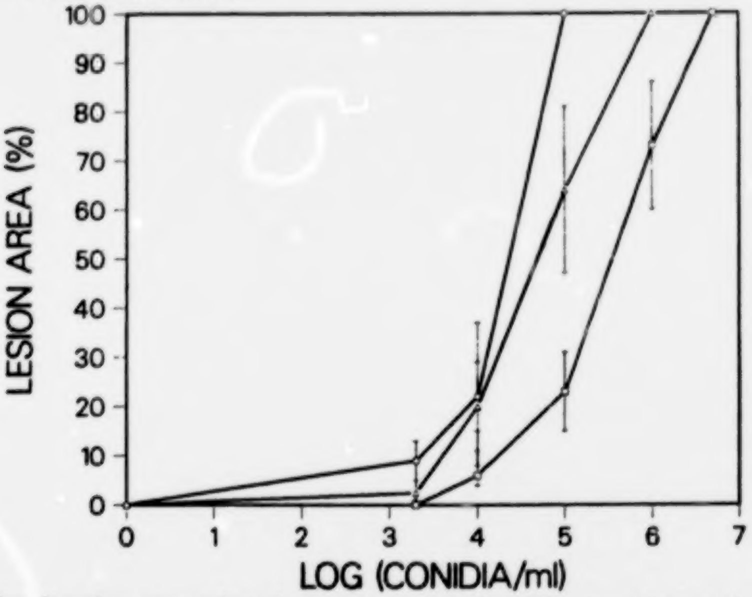

Fig. 3. Effect of inoculum concentration and temperature at time of inoculation on establishment of infections of *C. pycnocephalus* L. by *Alternaria* sp. Plants were inoculated with spore suspensions of different concentrations shown on the abscissa and then held in a mist chamber for 24 h at 5°C (□), 13°C (△), or 20°C (○). Symptom development occurred under subsequent standard greenhouse conditions and was measured after 7 days.

This isolate of *Alternaria* shows promise as a biological control agent of *C. pycnocephalus*. Among the advantages of applying this endemic pathogen as a mycoherbicide are a very narrow host range, ease in obtaining and storing large quantities of spores, ease in application of the spores, and effectiveness of control of the cotyledon stage of growth. Further studies are needed to determine factors which will allow high infection efficiency at lower inoculum concentrations. Field inoculations should consider the age of the thistle, the duration of moisture on the leaf surface and temperature at the time of inoculation to optimize infection with this fungus.

Acknowledgments

We wish to thank Marisa D'Angeli and Dan Moscow for their technical assistance.

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Evaluation of Plant Pathogens in Europe for the Biological Control of Introduced Weed Species in North America

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Abstract

A cooperative agreement was initiated in 1980 to evaluate potential of plant pathogens for biological control of introduced weed species in the United States. The agreement, between the United States Department of Agriculture-Agricultural Research Service and the Eidgenossische Technische Hochschule in Zurich, Switzerland, makes it possible for continuous research on biological control of weeds with plant pathogens in locations where many of the introduced North American plant species are native. Collection and evaluation of plant pathogens for the control of leafy spurge (*Euphorbia esula-virgata*) are a major part of the research effort. Studies on *Uromyces* species, which cause rust disease of spurges, are of particular interest because infections by these species are systemic and potentially very destructive. Additional field studies are under way in Europe to quantify infection and stress of artichokes and *Cirsium* spp. native to North America that are caused by the rust fungus, *Puccinia carduorum*.

Evaluation d'Agents Pathogènes pour les Besoins du Contrôle Biologique de Mauvaises Herbes Introduites en Amérique du Nord

Un accord de co-opération a été conclu en 1980 afin d'évaluer le potentiel en matière des phytopathogènes en vue de la lutte biologique contre certaines mauvaises herbes introduites aux Etats-Unis. Cet accord, conclu entre le Department of Agriculture-Agricultural Research Service des Etats-Unis et l'Eidgenossische Technischer Hochschule de Zurich, Suisse, rend possible la recherche continue sur le biocontrôle au moyen d'agents pathogènes, de plantes nuisibles sur des sites où beaucoup des espèces de plantes introduites en Amérique du Nord sont indigènes. La récolte et l'évaluation d'agents pathogènes pour le contrôle de l'euphorbe touffue (*Euphorbia esula-virgata*) constituent une partie majeure de cette recherche. Des études sur des espèces d'*Uromyces*, rouilles attaquant les euphorbes, sont d'un interêt particulier, à cause de la nature systémique des infections par ces espèces et de la destruction qu'elles peuvent causer. D'autres études sur le terrain sont en cours en Europe, afin de mesurer l'importance de l'infection et du stress causés par la rouille *Puccinia carduorum*, aux artichauts et aux espèces de *Cirsium*, indigènes en Amérique du Nord.

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Susceptibility of *Cynara scolymus* (Artichoke) to *Puccinia carduorum* Observed under Greenhouse Conditions

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Abstract

An isolate of *Puccinia carduorum* from Turkey was evaluated for biological control of *Carduus nutans* (musk thistle) in the United States. In a greenhouse study, the host range of *P. carduorum* was found limited to the subtribe Carduinae (Cynareae tribe, Asteraceae), including artichoke (*Cynara scolymus*) and a few species of *Cirsium*. Infection on artichoke was quantified because of the economic importance of this plant. Results indicate that artichoke, grown from seed or crown, is always less susceptible than musk thistle given similar conditions. Artichoke seedlings (cotyledons and first true leaves) are more susceptible than older plants from seed (third and fifth true leaves). These data suggest artichoke production will not be threatened by *P. carduorum*, if the fungus is approved for biological control of musk thistle.

Vulnérabilité de *Cynara scolymus* (Artichaut) au *Puccinia carduorum* en Serre

On a évalué les possibilités d'utilisation d'un isolat de *Puccinia carduorum* d'Eurasie comme agent biologique potentiel pour la lutte contre *Carduus nutans* (chardon penchi). Au cours d'une étude en serre, les hôtes de ce champignon de la rouille se sont limités à la tribu Cynareae (Astéracées) qui comprend le chardon *C. nutans* et l'artichaut. De jeunes plants d'artichaut (*Cynara scolymus*) (âgés de trois semaines) de 27 lignés étaient vulnérables au *P. carduorum*, tandis que les plantes âgés de six semaines et ceux ayant atteint la maturité (à partir des couronnes) (âgés de six mois) étaient plus résistants. Un isolat de *Carduus tenuiflorus* (chardon à minces fleurs) de la Californie, identifié comme *P. carduorum* par D.B.O. Savile, Canada, a infecté les jeunes plants d'artichauts, sur lesquels ont été observés des télias, mais non pas des urédinales. Cet isolat n'a pas été relevé sur les plants d'artichaut en Californie. En outre on n'a pas documenté d'infections par *P. carduorum* sur les artichauts en Eurasie. Par conséquent, il semble que les artichauts ne sont vulnérables au *P. carduorum* qu'en serre. L'introduction de *P. carduorum* comme agent biolgique de lutte contre *C. nutans* en Amérique du Nord ne nuirait probablement pas à la production d'artichauts.

Introduction

Musk thistle, *Carduus nutans* L. spp. *leiophyllus* (Petrovic) Stoj. & Stef. (*sensu* Moore and Frankton 1974) (Compositae), is an introduced weed in the United States. It is an important pest or threat in 15% of the counties in the U.S. (Dunn 1976). Use of natural enemies to control musk thistle in the U.S. began in 1969 with the release of *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae), a seed-head weevil (Kok 1981). Although significant reduction in stands has resulted from the use of *R. conicus* alone, additional stress of musk thistle is desirable, particularly in situations where flowering of musk thistle and weevil activity are out of synchrony.

Currently the rust fungus *Puccinia carduorum* Jacq. (Uredinales) is being evaluated at the Plant Disease Research Laboratory (PDRL) for use in biological control of musk thistle. The pathogen is very aggressive on musk thistle and seems well suited to environmental conditions in North America (Politis and Bruckart 1983). Host range studies indicate that other plant genera belonging to the subtribe Carduinae in the tribe Cynareae are susceptible to the rust fungus under conditions occurring in the containment facility at Frederick, MD (Politis *et al.* 1984). One of these is artichoke (*Cynara scolymus* L.; Compositae), a related plant of economic importance, particularly in California, U.S.A. (Ryder *et al.* 1983).

The objective of this research was to characterize and quantify infection of artichoke and to compare these data with those from musk thistle inoculated and grown under the same conditions.

Materials and Methods

Propagative material of artichoke was obtained from California and consisted of both crowns and seeds. Musk thistle plants were grown from seed collected in Frederick MD.

All plants were inoculated with urediniospores of *P. carduorum*, isolate III, collected in Turkey by R.G. Emge in 1978. A turntable settling tower (Melching 1967) was used to insure uniform distribution of inoculum over plant surfaces. Two mg of freshly harvested urediniospores/eight plants were used during inoculation. Plants were placed inside a dew chamber for 16 h following inoculation and then grown in a greenhouse for 2 wks before data were collected. Details of propagation and inoculation recently have been described (Politis *et al.* 1984).

Susceptibility of Artichokes and Musk Thistle

The first experiment involved artichoke plants grown from crowns in 20 cm pots. Every 2 wks a set of six plants was cut back to the soil line. Two wks after the fourth set was cut back, all the plants were inoculated. Thus leaves representing 2-, 4-, 6-, and 8-wk-old tissue were inoculated; musk thistle 6 wks after planting was inoculated for comparison.

Susceptibility of artichoke from seed was evaluated in the second experiment by planting 27 artichoke breeding lines and inoculating plants at each of four growth stages: cotyledonary; first true leaf; third true leaf; and fifth true leaf. A set of musk thistle plants received the same treatment for comparison.

Quantification and Characterization of Infection

Two wks following each inoculation, inoculated leaves were removed from the plants, pustules were counted, and leaf areas measured using a Lambda Area Meter, an electronic leaf area instrument (LI-COR, Inc., Lincoln, NE). In the experiment with artichoke from crowns, confidence intervals were calculated for statistical comparison of treatments. Artichoke breeding lines from seed were compared statistically using Tukey's analysis (Steel and Torrie 1960).

To compare more precisely relative infection of musk thistle and artichoke grown from seed, pustule diameters were measured for 100 pustules each on artichoke and musk thistle. From this, leaf area infected for each species was determined and Tukey's analysis was used for statistical comparison.

Results and Discussion

In every test, musk thistle had distinctly more pustules/unit leaf area than artichoke from either seed or crowns. Differences were statistically significant between musk thistle and all treatments involving artichoke from crowns; the average number of pustules/cm^2 was 0.025 for all artichoke treatments and 1.18 for musk thistle (Table 1).

Differences between musk thistle and artichoke from seed also were statistically significant in 91 of 96 comparisons (Table 2). Where differences were not statistically significant, there were distinctly fewer pustules on artichoke than on musk thistle. The average number of pustules/cm^2 on all artichoke breeding lines at each leaf stage (mean of the means) was: 1.81 for cotyledons and 1.74, 0.40, and 0.15 for first, third, and fifth true leaves, respectively, which indicates an increase in artichoke resistance with plant development (each leaf was inoculated when fully expanded). The comparable figures for musk thistle are: 4.28, 8.52, 1.95 and 7.61 pustules/cm^2, indicating no change in susceptibility with plant development to the fifth true leaf. Leaf area infected for fifth true leaves was calculated on the basis of pustule diameter of 0.20 mm for artichoke and 0.34 mm for musk thistle. Values calculated for leaf area infected based on these measurements are less than 0.2 mm^2/cm^2 leaf tissue for artichoke and 6.91 mm^2/cm^2 for musk thistle.

Artichoke is much less susceptible than musk thistle when conditions of inoculation and environment are the same. These differences between artichoke and musk thistle occur regardless of stage in plant development, even though leaves on young artichoke plants from seed are much more susceptible than leaves developing later. Differences in susceptibility of the two species occur regardless of method of propagation. Differences in leaf area infected of musk thistle and artichoke are even more distinct, since pustules which develop on musk thistle are 70% larger than on artichoke. Artichoke grown from crown was infected at a level similar to infection on fifth true leaves.

On the basis of these data, artichokes do not seem threatened by the strain of *P. carduorum* currently studied at PDRL. Furthermore, several attempts to maintain *P. carduorum* on artichoke have never been successful. The indication is that, although artichoke is susceptible to *P. carduorum* under greenhouse conditions, limited inoculum production from infected artichoke and low efficiency of *P. carduorum* in infecting artichoke minimizes the probability that an artichoke 'strain' of the rust fungus will be selected. In Eurasia, where artichoke and diseased musk thistle are sympatric, there has never been a rust reported on artichoke (Gäumann 1959; Sydow and Sydow 1904).

The experience with *P. carduorum* on artichoke is similar to reported experiences with *Ceuthorhynchus trimaculatus* F. (Coleoptera: Curculionidae), a weevil evaluated for control of *Carduus* species (Compositae) (Kok 1975; Kok *et al.* 1979), and *Paranguina picridis* Kirjanova & Ivanova (Nematoda: Tylenchidae), a nematode evaluated for control of *Acroptilon* (= *Centaurea*) *repens* L. (Compositae) (Watson 1981). In both cases, artichoke was attacked by the candidate biocontrol agent. Resistance developed in artichoke as a result of attack and damage by each of these natural enemies was insignificant, so artichokes were considered as not seriously threatened. The same conclusion may be reached for *P. carduorum*; it is not a threat to artichoke production based upon: (1) greenhouse findings at the PDRL; and (2) the literature.

Acknowledgments

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Table 1. Number of pustules of *Puccinia carduorum* Jacq./cm^2 leaf tissue on musk thistle grown from seed and artichoke grown from crowns.

Treatment	Plant age (wk)	No. pust./cm^2 ±CI[1] Rep I	Rep II
Musk thistle	6	1.37 ±0.74	1.00 ±0.35
Artichoke			
CA-8	8	0.00	0.00
CA-6	6	0.04 ±0.14	0.07 ±0.10
CA-4	4	0.04 ±0.06	0.00
CA-2	2	0.05 ±0.12	0.00

[1] $P < 0.05$

Table 2. Number of pustules of *Puccinia carduorum* Jacq./cm^2 leaf tissue on musk thistle and artichoke grown from seed.[1,2]

		Leaf Stage		
Plant	Cotyledon	1st T.L.[3]	3rd T.L.	5th T.L.
Musk thistle	4.28 *a*	8.52 *a*	1.95 *a*	7.61*a*
Artichoke				
BT-3	1.39 *cd*	1.41 *cd*	0.30 *b*	0.14*b*
BT-8	1.19 *cd*	1.73 *cd*	1.08*ab*	0.06*b*
CAM-0	1.61*bcd*	1.17 *cd*	0.14 *b*	0.01*b*
CAM-7	1.64*bcd*	0.81 *d*	0.41 *b*	0.33*b*
CAS-1	1.81*bcd*	1.72 *cd*	1.03*ab*	0.36*b*
CAT-4	1.59*bcd*	1.69 *cd*	0.06 *b*	0.02*b*
CENT-0	2.44*bcd*	2.45*bcd*	0.64 *b*	0.07*b*
CENT-2		3.84 *b*	0.26 *b*	0.30*b*
GG-8	1.68*bcd*	1.36 *cd*	0.43 *b*	0.07*b*
GG-10			0.41 *b*	0.13*b*
Green Globe	3.25 *ab*	1.12 *cd*	0.55 *b*	0.14*b*
GROS-0	2.45*bcd*	1.46 *cd*	0.27 *b*	0.02*b*
GROS-5	2.44*bcd*	2.21*bcd*	0.72 *b*	
LOCO-0		2.23*bcd*	0.46 *b*	0.15*b*
LOCO-8	1.34 *cd*	1.49 *cd*	0.06 *b*	0.01*b*
MAZ-4		2.26*bcd*	0.54 *b*	0.01*b*
MAZ-8	1.89*bcd*	1.58 *cd*	0.14 *b*	0.18*b*
NTN-4	1.54 *cd*	2.24*bcd*	0.22 *b*	0.05*b*
NTN-8	1.29 *cd*	1.09 *cd*	0.95*ab*	0.02*b*
ROMA-1	1.40 *cd*	1.90*bcd*	0.10 *b*	0.03*b*
ROMA-4	2.17*bcd*	2.81 *bc*	0.52 *b*	0.04*b*
SCAR-0			0.28 *b*	0.01*b*
SS-4	1.99*bcd*	1.52 *cd*	0.05 *b*	0.07*b*
VERO-0	2.11*bcd*	1.71 *cd*	0.23 *b*	0.01*b*
VERP-10	2.68*abc*	1.48 *cd*	0.52 *b*	1.52*b*
VIP-5	1.12 *cd*	0.65 *d*	0.38 *b*	0.04*b*
VIP-8	0.85 *d*	1.60 *cd*	0.20 *b*	0.22*b*

[1] Plants uniformly inoculated in a turntable settling tower.

[2] Means compared using Tukey's analysis within leaf stage treatments, $P<0.05$.

[3] T.L. = true leaf.

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Occurrence and Spread of *Phragmidium violaceum* on Blackberry (*Rubus fruticosus*) in Victoria, Australia

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Abstract

The rust fungus *Phragmidium violaceum* which was being considered for the biological control of European blackberry (*Rubus fruticosus* agg.) in Australia, was recorded as being present in Victoria in February 1984. Several distinct, heavily infested sites were found indicating that the fungus was probably deliberately introduced, thus contravening Australian plant quarantine laws. Spread of the rust has been rapid. Field observations and laboratory inoculations have shown six species of European blackberry to be susceptible while two are resistant. The implications of the results are discussed.

Répartition et Dissémination de *Phragmidium violaceum* sur les Ronces (*Rubus fruticosus*) à Victoria, en Australie

En Europe, on a évalué les possibilités d'utilisation du champignon de la rouille *Phragmidium violaceum* pour la lutte biologique contre les ronces (*Rubus fruticosus* agg.) en Australie. À la fin de février 1984, la présence du champignon a été relevée à Victoria. Plusieurs sites distincts, fortement infestés, ont été repérés, ce qui indique que le champignon a sans doute été introduit intentionnellement, malgré les lois australiennes sur la quarantaine des plantes. On surveille actuellement la dissémination de la rouille et ses effets virulents sur la plante nuisible.

Introduction

The rust fungus *Phragmidium violaceum* (Schultz) Winter (Uredinales) was studied in Europe between 1978 and 1983 to determine its suitability for the biological control of European blackberry (*Rubus fruticosus* L. agg.; Rosaceae) in Australia. The investigations showed that this autoecious and macrocyclic rust is highly damaging to eight species and several hybrids of *R. fruticosus* naturalized in Australia and that it is sufficiently specific to these weeds (Bruzzese and Hasan, unpubl. data). It was therefore concluded that the rust's introduction to Australia would be desirable. Submissions were being prepared to have the weed approved as a candidate weed for biological control (Field and Bruzzese 1985) and to seek approval from the Federal Department of Primary Industry for introduction of the rust. However, the rust was identified as being present in southern Victoria in late February 1984 (Marks *et al.* 1984), before these approvals could be obtained. This article describes and gives the preliminary results of a survey carried out to study the spread of the rust in Victoria.

Methods and Materials

Early Inspections

The day after *P. violaceum* was identified, the site of first discovery in south Gippsland was visited by officers of the Department of Conservation, Forests and Lands. An inspection of the Albert River valley near the township of Hiawatha showed several heavily infected European blackberry brambles along the road in the valley. These brambles were in the early stages of defoliation and were quite distinct from adjoining brambles which were only lightly infected. After the inspection it was concluded that the pathogen had been in this area for a short time (probably 6–8 wks), that it was probably deliberately distributed as all the heavily infected brambles were in accessible situations, and that eradication of the infestations was impossible as although the main infestations were localized, individual pustules were found on blackberry over a distance of about 10 km along the valley.

Two days later, another outbreak of the rust was reported from the Dandenong Ranges east of Melbourne. Upon inspection of the area only one heavily infected bramble was found in the main street of the township of Olinda. Individual pustules and light infestations were found over an area of about 100 km^2

The infections at Olinda and Hiawatha, which are 130 km apart, seemed to be of the same age. The possibility then arose that several other release sites occurred in these or other parts of Victoria.

Survey of Occurrence and Spread

Assuming that the rust was deliberately and therefore illegally introduced, there was a strong possibility that this was done on plant material. It was therefore possible that other less specific plant pathogens or arthropods may have also been introduced. A survey was therefore planned with the following aims: (1) discover other possible release sites of the rust in Victoria; (2) identify undesirable organisms which may have also been introduced; (3) study the spread of the rust; and (4) find which species of blackberry were susceptible to the rust.

Field officers of the Department of Conservation, Forests and Lands were asked to carry out the survey in their districts. A meeting was held in each Senior Land Management Officer's district within 2 wks of the discovery of the rust. All Land Management Officers, District Foresters and National Parks Rangers in charge of public land in the district were invited to attend the meeting. Each officer was issued with a detailed description of *P. violaceum*, a 24 × 20 cm photograph showing different stages of infection on blackberry leaves, detailed instructions on the procedure for the survey, and questionnaires for each site in their districts. Each officer was asked to select five blackberry sites in each Parish of their district which were to be inspected for the presence or absence of rust. If *P. violaceum* was thought to be present, the attack was to be ranked as heavy (brambles defoliated), common (pustules on most leaves) or rare (occasional pustules on a bramble). This information was used to decide if the site was a possible release area, or close to one. A sample of a few leaves representative of the infection were requested with the questionnaire to enable the identification of the pathogen and in most cases, that of the blackberry.

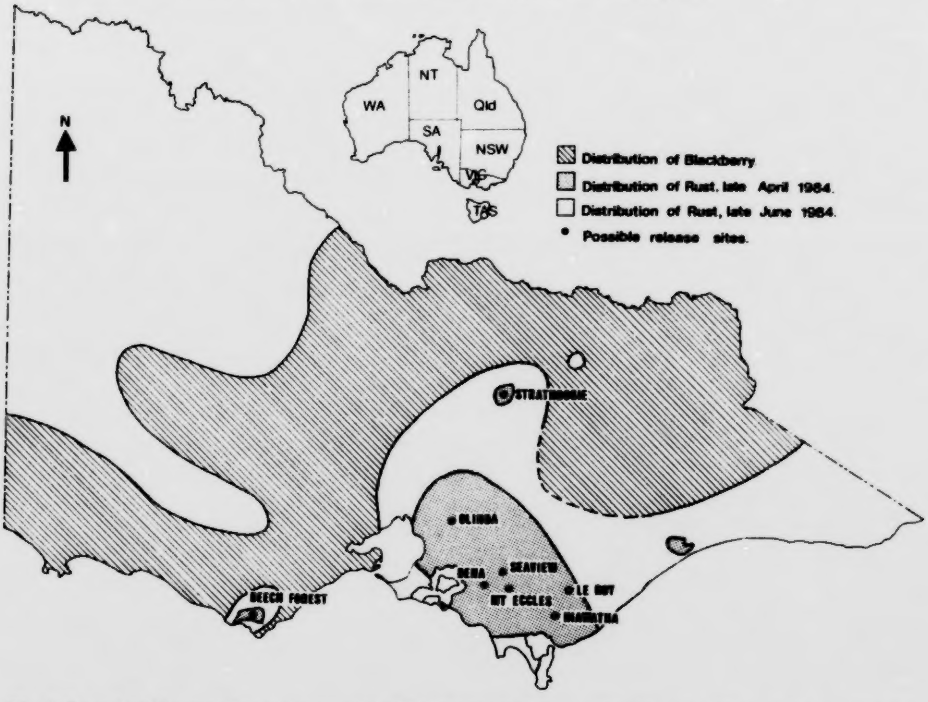
Officers were asked to complete the first inspection by mid-April. Another inspection at the same sites was carried out in June and one is planned for November 1984. These will enable the spread of the rust in Victoria to be studied.

Media Campaign

Soon after the rust was discovered, the media was informed through a press release made by the Minister for Conservation, Forests and Lands. The public was asked to supply any information which may be of importance in establishing how the rust entered Australia and where it was released. Subsequent press releases were made to keep the public informed on the spread of the rust and as a reminder of the interest in how the rust entered Australia.

Results and Discussion

The early inspections and the April survey showed that *P. violaceum* appeared to be released at a number of sites in Victoria (Fig. 1). Release seemed to be concentrated in south Gippsland where 17 possible release sites were found (13 at Hiawatha and one each at LeRoy, Seaview, Mt. Eccles and Bena). Other possible release sites in Victoria were in the Dandenong ranges (two at Olinda), Otway ranges (two at Beech Forest) and Strathbogie ranges (one at Strathbogie). Inspection of these sites has not yet revealed evidence of other introduced pathogens or arthropods.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▨ Distribution of Blackberry
☐ Distribution of Rust, late April 1984.
☐ Distribution of Rust, late June 1984.
• Possible release sites.
STRATHBOGIE
OLINDA
BENA
SEAVIEW
MT ECCLES
LE ROY
HIAWATHA
BEECH FOREST

Fig. 1. Spread of *Phragmidium violaceum* (Schultz) Winter on European blackberry in Victoria, February–June 1984.

The April survey showed that the rust spread very rapidly. Questionnaires for 1666 sites throughout Victoria's blackberry range were received and positive identification of the rust was made at 244 sites. It also showed that the south Gippsland and Dandenong ranges infestations had merged but those of the Otway and Strathbogie ranges ramained isolated (Fig. 1). The questionnaires for the June survey indicate that considerable spread has occurred during the autumn months (Fig. 1). Also, most samples received in June showed that the rust was producing overwintering spores indicating that for this growing season, spread of the rust has ceased.

The leaf samples received show that four species of blackberry have been attacked. These are *Rubus procerus* P.J. Muell., *R. polyanthemus* Lindeb., *R. laciniatus* Willd., and some *R. ulmifolius* Schott hybrids. Laboratory inoculations of the eight European blackberry species naturalized in Victoria has confirmed the observations from field collected specimens. The inoculations have also shown that *R. ulmifolius* and *R. vestitus* Weihe & Nees are susceptible to the rust but that *R. cissburiensis* Barton & Riddels, *R. rosaceus* Weihe & Nees and some *R. ulmifolius* hybrids are highly resistant to this strain(s) of the rust. Further studies are underway which will quantify the effect of the rust on blackberry species. The results will indicate whether there is a need to import other selected strains of *P. violaceum*.

Whilst the media campaign has not yet yielded information on how the rust entered Australia, it was helpful with information on the spread of the rust. Reports were received from as far as northeastern New South Wales where the rust was first recorded in early June. Here it was released by farmers who imported the rust from Victoria (J.E. Cherry, pers. comm., 1984).

Acknowledgments

We thank all the officers of the Department of Conservation, Forests and Lands who assisted with the survey.

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Occurrence and Identification of Some Weed Diseases and their Consideration for Biological Weed Control

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Abstract

Surveys were initiated to gather information on the occurrence and distribution of diseases of weeds in Louisiana soybean fields. Causal fungi were isolated and identified and tests begun for consideration of these pathogens as potential biological control agents. The following fungi were found mildly virulent in pathogenicity tests: *Helminthosporium* and *Phoma* from signal grass; *Phoma* from eclipta; *Alternaria* and *Colletotrichum* from morning glory; *Helminthosporium* from itchgrass; *Alternaria* and *Phomopsis* from curly dock; *Phoma* from hemp sesbania; *Phomopsis* from prickly sida; *Colletotrichum*, *Phoma*, and *Sphacelotheca* from johnsongrass. The *Phoma* sp. from *Eclipta alba* caused severe blight and may be worthy of further study. Johnsongrass loose smut stunted plants and prevented seed set and appears to be a potential biocontrol candidate. Initial host range studies showed the smut pathogenic only on johnsongrass. It was non-pathogenic on soybean and sorghum varieties tested to date.

L'Incidence et l'Identification de quelques Maladies de Mauvaises Herbes et leur Potentiel comme moyen de Biocontrôle

On a entrepris des enquêtes en vue de recueillir des donnés concernant l'incidence et la répartition des maladies de mauvaises herbes dans des plantations de soja dans l'état de Louisiana. Des champignons ont été isolés et des essais ont été mis en oeuvre pour déterminer leurs possibilités en tant qu'agents de biocontrôle. Au cours d'ésais de pathogénicité, les espèces suivantes de champignons ont demontré une virulence modérée: *Helminthosporum* et *Phoma* provenant de 'signal grass'; *Phoma* d'*Eclipta*; *Alternaria* et *Colletotrichum* de volubilis; *Helmonthosporum* d''itchgrass'; *Alternaria* et *Phomopsis* d'oseille sauvage; *Phoma* de 'hemp sesbania'; *Phomopsis* de 'prickly sida'; *Colletotrichum*, *Phoma* et *Sphacelotheca* de 'johnsongrass'. L'espèce de *Phoma* provenant d'*Eclipta alba* était responsable d'une nielle sévère et pourrait justifier une étude plus prolongée. La nielle du 'johnsongrass' qui fait rabougrir les plantes et empêche la maturation des graines, paraît présenter des possibilités en matière de biocontrôle. Les premières études sur 'léventail des plantes-hôtes ont indiqué que cette nielle est pathogène seulement dans le cas du 'johnsongrass', et n'affecte aucune des varietés du soja et de sorgho examinées jusqu'ici.

Introduction

Plant pathogens are beginning to receive serious attention as potential agents for biological control of weeds (Templeton and Smith 1977; Wilson 1969). Considerable success has been achieved by the practical development of a *Colletotrichum* sp. (Melanconiales) as a mycoherbicide for controlling northern jointvetch (*Aeschynomene virginica* [L.] B.S.P.; Leguminosae) in rice (Daniel *et al.* 1973; Templeton *et al.* 1976). *Cercospora rodmanii* Conway (Hyphomycetes) has been tested on waterhyacinth (*Eichhornia crassipes* [Mart.] Solms-Laubach; Pontederiaceae) in Florida and Louisiana

(Conway 1976; Freeman 1977). Several other aquatic weed problems are being studied (Freeman 1977; Zettler and Freeman 1972). Additional emphasis has been placed on this area of research by the recent approval of a regional project on use of fungi as biocontrol agents of weeds (USDA 1978).

Studies on occurrence, distribution and identification of causal agents of diseases on important weeds in soybean fields were conducted in Louisiana. We report here on these survey results and on preliminary inoculation and host range studies with some of the fungi, including a head smut of johnsongrass (*Sorghum halepense* [L.] Pers.; Gramineae).

Materials and Methods

Disease surveys were carried out on weeds in soybean fields during the growing season in the following Louisiana parishes: Concordia, East Baton Rouge, East Carrol, West Carrol, Lafayette, Rapides, St. Landry, Tensas, Union, and West Feliciana. Leafspots, blights and stem diseases were sought during the surveys. The causal agents, especially fungi, were isolated on acidified potato dextrose agar (Difco), V-8 juice agar (170 ml juice and 3 g calcium carbonate/*l*, rabbit food agar (25 g/*l*), and malt-yeast-dextrose agar (MYD, 10 g malt, 1 g yeast extract, and 10 g dextrose/*l*). MYD and V-8 agars were supplemented with 50 mg/*l* chloramphenicol and used for isolation and growth of the chlamydospores from johnsongrass loose smut and the covered smut from junglerice. All fungal isolates, except the smuts, were grown at room temperature (*c.* 25°C). Two-wk-old, liquid cultures of isolates of fungi in the genera *Alternaria* (Hyphomycetes), *Colletotrichum*, *Helminthosporium* (Hyphomycetes), *Phoma* (Coelomycetes), and *Phomopsis* (Coelomycetes) were used in greenhouse pathogenicity tests. Inoculum was prepared by blending the liquid cultures for 5 min in a sorvall Omni-Mixer. All inocula were sprayed onto 1-, 4- and 8-week-old test weeds.

The smut fungi *Sphacelotheca* and *Tolyposporium* (both Ustilaginales) were grown in an incubator at 32°C for the first 24 h, after which developing smut colonies were transferred to fresh medium. Sporidial suspensions were obtained by transferring mycelial and sporidial masses from agar medium to liquid MYD or V-8 media. These cultures were shaken on a reciprocal shaker for 24 h at room temperature. The resulting sporidial suspensions were used to inoculate test plants by spray inoculation or by hypodermic syringe injections into their stems. Limited host range studies were carried out with the johnsongrass smut on several soybean varieties (Bragg, Coker, Coker 136, Dare, Forrest, Hood 75, Lancer, Lee 74, Jarravig, Ranson and Tracy), sorghum (Paymaster R 1090), corn, rye, Japanese millet and shattercane. Observations were made for up to five months on test plants inoculated with the smut fungi.

Results and Discussion

Numerous foliage diseases were observed on weeds in soybean fields during the surveys. White and red rusts caused by *Albugo* (Peronosporales) and *Coleosporium* (Uredinales) spp. were observed on morning glory (*Ipomoea hederacea* [L.] Jacq.; Convolvulaceae). A rust was also collected on cocklebur (*Xanthium pennsylvanicum* Walln.; Compositae). The fungi isolated in pure culture from 12 common weeds are listed in Table 1 with their respective weed hosts.

The following fungi were used in pathogenicity tests and gave positive results, but most were only mildly virulent: *Helminthosporium* and *Phomas* spp. from broadleaf signal grass (*Brachiaria platyphylla* [Griseb.] Nash; Gramineae); *Tolyposporium* from junglerice (*Echinochloa colonum* [L.] Link; Gramineae); *Phoma* from eclipta (*Eclipta* *alba* [L.] Hassk.; Gramineae); *Alternaria* and *Colletotrichum* from ivyleaf morning glory; *Helminthosporium* from itchgrass (*Rottboellia exaltata* L.; Gramineae); *Alternaria* and *Phomopsis* from curly dock (*Rumex crispus* L.; Polygonaceae); *Phoma* from hemp sesbania (*Sesbania exaltata* [Raf.] Cory; Leguminosae); *Phomopsis* from prickly sida (*Sida spinosa* L.; Malvaceae); *Colletotrichum*, *Phoma*, and *Sphacelotheca* from johnsongrass. Additional screening tests will have to be made before these fungi are discarded from further consideration as biocontrol agents.

Table 1. Weed hosts and fungi isolated from diseased specimens.

Host plant	Fungi isolated	Pathogenicity
Brachiaria platyphylla (Griseb.) Nash. (signalgrass)	*Helminthosporium*, *Phoma*	positive
Cucumis melo L. (smell melon)	*Alternaria*	•
Echinochloa colonum (L.) Link (junglerice)	*Tolyposporium*	positive
Eclipta alba (L.) Hassk. (eclipta)	*Phoma*	positive
	Alternaria, *Phomopsis*	•
Euphorbia heterophylla L. (poinsettia)	*Phoma*	•
Ipomoea hederacea (L.) Jacq. (morningglory)	*Alternaria*, *Colletotrichum*	positive
	Cercospora	•
Rottboellia exaltata L. (itchgrass)	*Helminthosporium*	positive
Rumex crispus L. (curly dock)	*Alternaria*, *Phomopsis*	positive
Sesbania exaltata (Raf.) Cory (hemp sesbania)	*Alternaria*, *Helminthosporium*	•
	Phoma	positive
Sida spinosa L. (prickly sida)	*Phomopsis*	positive
Sorghum halepense (L.) Pers. (johnsongrass)	*Colletotrichum*, *Phyllosticta*	positive
	Sphacelotheca cruenta	positive
	Alternaria, *Fusarium*	•
Xanthium pennsylvanicum Wallr. (cocklebur)	*Alternaria*, *Phoma*	•

• Pathogenicity tests not performed with these fungi.

The *Phoma* sp. from *E. alba* caused a severe blight on 2–3-wk-old plants 1 wk after inoculation. This fungus appears to warrant further serious testing. Johnsongrass smut, caused by *Sphacelotheca cruenta* (Kuehn) Potter, was pathogenic (by both injection and spray inoculations) and caused plant stunting and smutting of the seed heads. The systemic nature of this disease in preventing seed production year after year might be an advantage in further consideration of this fungus as a biocontrol agent. Initial host range studies indicate that our current isolate is pathogenic only on johnsongrass. Additional studies are needed to confirm that the smut will not infect commercial sorghum varieties or other cereals.

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Prospects for Biological Control of *Heliotropium europaeum* by Fungal Pathogens

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Abstract

The summer annual, common heliotrope, *Heliotropium europaeum* (Boraginaceae), is a major weed in Australia causing severe stock poisoning. The weed is of Mediterranean and Middle Eastern origin. Surveys were therefore made in Europe, North Africa and the Middle East to discovery organisms which could act as biological control agents of this species. Among these agents, the rust fungus *Uromyces heliotropii* and the leaf spot caused by *Cercospora* sp. damaged the plant. Evaluation has been made of the biology and host range of *U. heliotropii* with a view to its use as a biological control agent of common heliotrope in Australia. In addition some preliminary data on the *Cercospora* sp. is presented.

Lutte Biologique contre *Helyotropium europaeum* par l'Utilisation de Champignons Pathogènes

L'espèce annuelle estivale, soit l'héliotrope d'Europe, *Heliotropium europaeum* (Boraginacées), est une plant nuisible importante en Australie, qui est hautement toxique pour le bétail et les moutons. Elle est originaire des pays méditerranéens et du Moyen-Orient. Des études ont donc été faites en Europe, en Afrique du Nord et au Moyen-Orient afin de trouver des organismes qui pourraient servir d'agents biologiques pour la lutte contre cette espèce. Parmi les divers insectes parasites et mycoses relevés, deux maladies fongiques sont nuisibles pour la plante. Il s'agit du champignon de la rouille *Uromyces heliotropii* et la tache des feuilles causée par *Cercospora* spp. La biologie et la gamme d'hôtes de ces agents pathogènes ont fait l'objet d'évaluations préliminaires en vue de déterminer leur efficacité comme agents biologiques de lutte contre l'héliotrope en Australie.

Introduction

Heliotropium europaeum L. (Boraginaceae), common heliotrope, is a summer-growing annual. The plant is native to the Mediterranean and Middle Eastern regions. Many species of *Heliotropium* other than *H. europaeum* are found in Iran and Iraq (Riedl 1967) suggesting that the genus may have evolved in the Palaearctic region. Common heliotrope was accidentally introduced into Australia where it has become an important weed (Everist 1974). It grows well in fallows and pastures especially after summer rains and causes poisoning due to the presence of pyrrolizidine alkaloids (Bull *et al.* 1956). The weed is also an effective competitor for moisture and consequently affects crop yield, especially in dry years (Delfosse and Cullen 1981). It multiplies only by seeds and these remain viable for many years in the soil.

Biological control seems to offer a promising alternative, as attempts to control common heliotrope by competition with other plants or with chemical herbicides have not been satisfactory. Surveys have been made in Europe, the Middle East and North

Africa and a number of insects and pathogens have been found to cause damage to *H. europaeum* and related species (Delfosse and Cullen 1981; Hasan and Cullen 1984). Among these, the flea beetle *Longitarsus albineus* Foudras (Coleoptera: Chrysomelidae) has already been studied in detail and introduced into Australia for the biological control of common heliotrope (Huber 1981). Drought prevented its establishment in the field (Delfosse 1985). Evaluation studies are now underway on the biological control potential of two fungal pathogens, *Uromyces heliotropii* Sredinski (Uredinales) and *Cercospora* sp. (Hyphomycetes).

Uromyces heliotropii

Distribution

U. heliotropii is a macrocyclic and autoecious rust fungus which infects common heliotrope in the Mediterranean and Middle Eastern regions. It has also been recorded from southern Russia (Gäumann 1959). The rust occurs in a wide variety of climates from cold continental parts of central Anatolia to some of the warmest areas of North Africa. It has never been recorded in Australia (McAlpine 1906; J. Walker, pers. comm., 1983).

Life Cycle

Observations in the field in Turkey have revealed that *U. heliotropii* remains active throughout the heliotrope season and attacks all stages and all aerial parts of *H. europaeum*. In early spring it appears as small, short, cylindrical, yellow aecidia in groups forming concentric rings, mostly on the lower surface of leaves of freshly germinated seedlings. Aecidia contain polygonoid to globoid, minutely, but densely verrucose, yellow aecidiospores. These aecidiospores in turn infect leaves and stems, producing dark brown, roundish uredinia exposed to the exterior by rupturing the epidermis (Fig. 1A). Uredinia are borne on both leaf surfaces but mostly on the upper surface. They are often large and abundant, giving rise to large quantities of powdery, brown, roundish to ellipsoid urediniospores (Fig. 1B). There are several generations of urediniospores throughout spring and summer, infection spreading rapidly on the already-infected plants and from plant to plant. In severe attacks, urediniospores cover entire leaves, causing rapid death of plant parts and, in the case of small plants and seedlings, the whole plant. Continuing production of uredinia on the stems and inflorescences of larger plants can also kill these or significantly retard their growth.

As the disease advances, dark, roundish to irregularly shaped telia appear among uredinia on leaves and stems. These contain unicellular, dark brown to black, thick-walled teliospores (Fig. 1C). The mature teliospores are capable of germinating immediately after they are produced. However, teliospores produced towards the end of the heliotrope season seem to overwinter, along with urediniospores, on dead plants and infect young seedlings the following season, producing spermagonia and aecidiospores. In turn, these infect more heliotrope and give rise to several generations of urediniospores.

Spore Germination and Germ Tube Growth

Urediniospores were seeded on the surface of water agar (1% Difco Bacto), plated on glass slides, in a spore settling tower (Chandreshekar and Heather 1981). Immediately

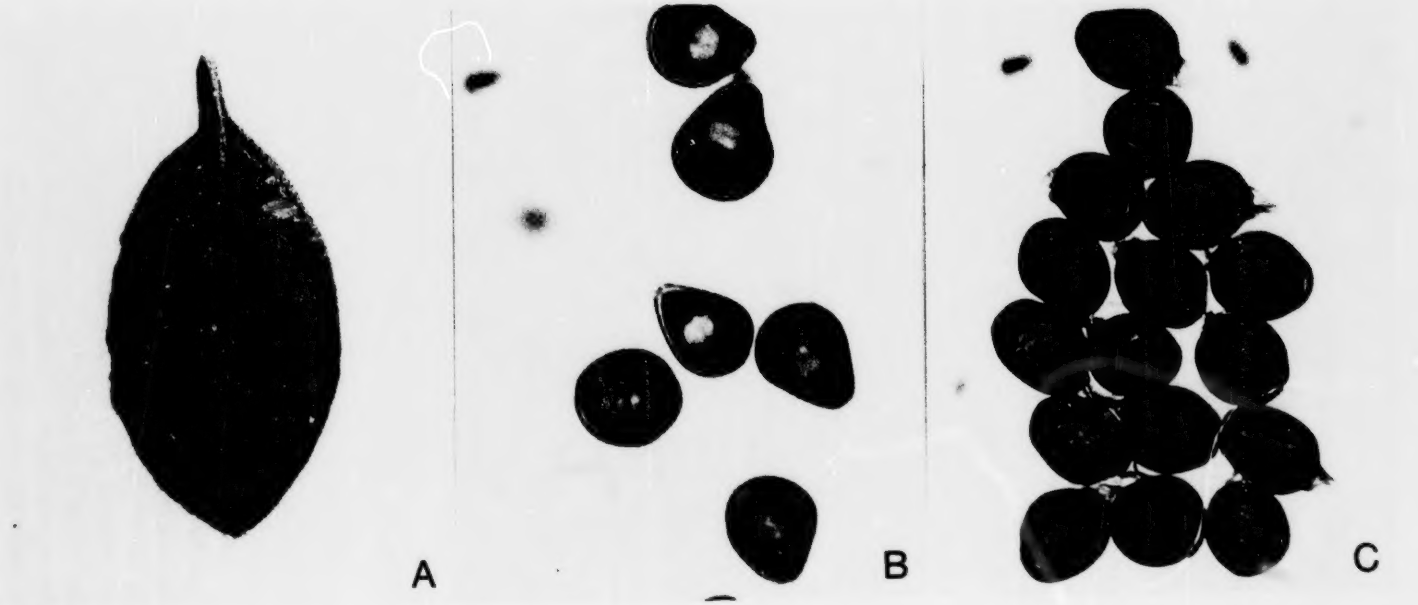

Fig. 1. *Uromyces heliotropii* Sredinski, the heliotrope rust. A. Uredinia on an infected leaf of common heliotrope, *Heliotropium europaeum* L. B. Urediniospores (× 600). C. Teliospores (× 600).

afterwards the slides were enclosed in plastic Petri dishes and incubated at required conditions.

Light and darkness. Agar plates with urediniospores were incubated in a phytotron at 20°C with continuous light (9288 lux) and 85% r.h. for 1, 2, 3, 4, 6, 8, and 24 h. Half the number of total plates were wrapped in aluminium foil and thus kept in darkness. Three replicates were used for each incubation period.

Urediniospores germinated both in continuous light and darkness (Table 1). However, darkness seemed to accelerate germination as a small number of spores germinated within 1 h, while it took about 2 h for spores to germinate in the light. Also in the dark, percent germination increased sharply, attaining maximum within 6 h, while in the light, maximum germination was obtained somewhere between 8 and 24 h. On the other hand, the rate of germ tube growth was higher in darkness than in light for incubation periods up to 8 h, but progressively increased, reaching maximum and equal levels at 24 h incubation both in light and darkness.

Table 1. Effect of light on percent germination and rate of germ tube growth of urediniospores of *Uromyces heliotropii* Sredinski at 20° C.

Hours of	Light		Darkness	
incubation	% Germination	Avg. length of germ tube (μm)	% Germination[1]	Avg. length of germ tube (μm)[2]
1	0	0	4.2	9
2	7.8	24	60.6	13
3	20.3	76	64.6	86
4	36.9	111	68.2	145
6	49.3	136	82.5	267
8	59.7	218	80.1	324
24	81.9	588	81.2	581

[1] Average counts of 600 spores.

[2] Average measure of 60 germ tubes.

Temperature. Agar plates were equilibrated at temperatures 5, 6, 8, 10, 15, 18, 20, 22, 25, 30, 32, and 35°C. Urediniospores were seeded on these equilibrated plates as described above and incubated for 5 and 24 h in darkness.

Good germination was obtained at temperatures between 18 and 30°C, being optimal at 25°C (Table 2). Urediniospores germinated at most of the temperatures but germination was inhibited at temperatures below 15°C. Only a few spores germinated at 6°C and 32°C. No germination occurred at 5° and 35°C.

Host Range

U. heliotropii has so far been recorded only on *H. europaeum* and related species, e.g. *H. eichwaldi* Steud. (= *H. ellipticum* Ledeb.) and *H. rotundifolium* Sieb. (Gäumann 1959). During surveys in Iran the rust was collected on *H. lasiocarpum* Fisch. & Mey. which is also considered to be a subspecies of *H. europaeum* (Brummitt 1972). Demonstration of the host specificity of *U. heliotropii* under laboratory conditions is being investigated in relation to Boraginaceae and related families (including plants of those families native to Australia) and crop plants. So far none of the test plants

Table 2. Percent germination and germ tube growth of urediniospores of *Uromyces heliotropii* Sredinski, at different temperatures in darkness.

	Hours of incubation			
	5		24	
Temperature (°C)	% Germination	Avg. length of germ tube (μm)	% Germination[1]	Avg. length of germ tube (μm)[2]
5	0	0	0	0
6	0	0	0.6	159
8	2.5	32	3.2	213
10	4.7	73	10.8	230
15	12.9	195	15.3	289
18	26.7	193	33.3	356
20	54.3	228	68.3	412
22	55.9	227	58.6	463
25	57.7	290	66.7	409
30	20.8	192	32.7	378
32	0.6	88	0	0
35	0	0	0	0

[1] Based on 600 spore counts in 3 replicates.

[2] Mean of 60 measures of germ tube in 3 replicates.

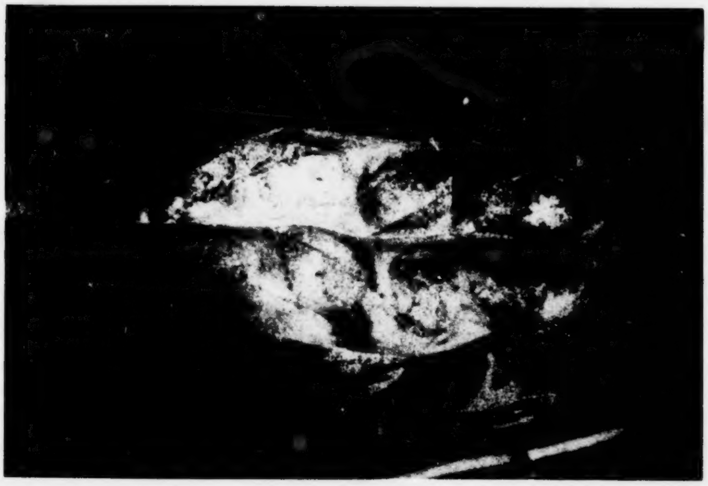

Fig. 2. Leaves of common heliotrope, *Heliotropium europaeum* L., bearing lesions caused by *Cercospora* sp.

including the ornamental *H. peruvianum* L. and the wild *H. curassavicum* L., which is found in the Mediterranean region, have been attacked by the rust fungus.

Cercospora spp.

Several *Cercospora* spp. have been recorded on *Heliotropium* in the Mediterranean region and elsewhere (Chupp 1953). One of these fungi has been found widely in heliotrope infestations in the Mediterranean and Middle Eastern regions (Hasan 1974). The pathogen multiplies only by asexual conidia and thus belongs to the group Hyphomycetes. It causes brown and circular to irregular lesions on leaves, sometimes covering the major portion of the leaf surface (Fig. 2). In these lesions are found brown stromata with pale, olivaceous conidiophores and conidia, mostly on the lower surface of the leaf. Conidia are multiseptate, hyaline, cylindric with subtruncate base and bluntly rounded tip.

The fungus has been grown on the culture medium Potato Dextrose Agar (Difco Bacto) with 0.5% yeast extract (Oxoid) and produces a non-sporulating mycelium mat. This, when fragmented in water and sprayed onto *H. europaeum*, produces sporulating lesions on leaves in the glasshouse. Similarly, infection was also obtained by spraying plants with a water suspension of conidia collected from the glasshouse or spontaneous field infections. The infected plants quickly lose their leaves and show poor growth or premature death.

Discussion

Observations in the field and glasshouse studies on the life cycle of *U. heliotropii* have confirmed that all four spore stages of the rust are produced on *H. europaeum*. This excludes the possibility of the pathogen having an alternate host. Also it seems to be highly damaging to the seedlings which is of great advantage as the weed begins to flower very early, and death of seedlings will reduce production of seeds, which is important for infestations of the weed.

Occurrence of common heliotrope depends very much upon conditions such as soil disturbance, absence of interspecific plant competition and adequate rainfall. This makes its distribution and abundance very unpredictable. In such a case a biological control agent has to be rapidly effective as well as able to survive and easily dispersed. The dry and powdery urediniospores are well adapted for easy dispersal by wind and thus have the capacity to reach heliotrope infestations even if these are far apart.

Better urediniospore germination in dark, and over a wide range of temperatures such as commonly prevail in common heliotrope infestations during the night, in presence of dew, are likely to be conducive to infection. Studies are, however, under way on effects of dew period and temperatures on infection of *H. europaeum*. Field experiments are also being conducted on the overwintering of the pathogen especially as the host weed is then absent in nature. If no environmental limitations are found and *U. heliotropii* proves to be host specific, its introduction to Australia for the biological control of the common heliotrope would be worthwhile.

It is too early to make predictions on the *Cercospora* sp. Studies are at present under way on the identification of this fungus, as three species of *Cercospora* are known to attack *Heliotropium* (Chupp 1953) and one of these, *C. taurica* Tranz., is already present in Australia (Delfosse 1985).

Acknowledgments

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Search in Greece and Turkey for *Puccinia chondrillina* Strains Suitable to Australian Forms of Skeleton Weed

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Abstract

Since introduction into Australia in 1971, strain IT-32 of the rust fungus *Puccinia chondrillina* from southern Italy has been extremely successful in controlling the most common, narrow-leaf, form of skeleton weed, but the remaining two forms of the weed remain unaffected. Strains virulent on these other forms of *Chondrillina juncea* have been sought. Very few spore samples from rust-infected plants collected in the western Mediterranean region infected the intermediate- or broad-leaf forms of the weed, so the area of the survey was extended to more eastern Mediterranean countries. Here several strains have been found to be virulent on the intermediate-leaf form. Two of these strains have recently been introduced into Australia for the biological control of this form of skeleton weed. A few strains with a low level of pathogenicity to the broad-leaf form have also been isolated from spore samples collected in Greece and Turkey, but the search for more virulent strains still continues.

Recherches en Grèce et en Turquie des Lignées de *Puccinia chondrillina* qui Constitueraient des Agents Biologiques Appropriés pour la Lutte contre les Espèces Australiennes d'Herbes Squelettes

Depuis son introduction en Australie en 1971, la lignée IT-32 du champignon *Puccinia chondrillina* qui provoque la rouille et qui provient du sud de l'Italie constitue un agent biologique extrêmement efficace pour la lutte contre l'espèce à mince feuille la plus commune d'herbe squelette, mais n'a eu aucun effet sur les deux autres formes de *Chondrilla juncea*. Par conséquent, il a été nécessaire de trouver des lignées virulentes pour ces deux dernières. Une fouille de la région méditerranéenne est demeurée vaine, très peu d'échantillons de spores recueillis dans l'ouest de la région ayant infecté les *C. juncea* à feuilles moyennes ou larges. Les recherches ont donc été portées dans des pays plus à l'est de la Méditerranée. On y a découvert plusieurs lignées virulentes pour la forme de *C. juncea* à feuilles moyennes et deux de ces lignées ont récemment été introduites en Australie en vue de lutter contre elle. Quelques lignées qui sont, dans une certaine mesure, pathogènes pour *C. juncea* à larges feuilles ont également été isolées dans les échantillons de spores recueillis en Grèce et en Turquie, mais on tente toujours de trouver des espèces encore plus virulentes.

Introduction

Following its introduction into Australia, the IT-32 strain of the rust fungus *Puccinia chondrillina* Bub. & Syd. (Uredinales) has been extremely successful and progressively reduced the population of the most common, narrow-leaf form of skeleton weed, *Chondrilla juncea* L. (Compositae) (Cullen *et al.* 1973; Cullen 1978; Hasan 1974; Hasan and Cullen 1984). As this form began to diminish, the other two forms, intermediate- and broad-leaf, which remained unaffected began to replace it in some areas. It was therefore considered necessary to search for the rust strains pathogenic to these other forms of the weed. Spore samples were collected from many sites in Europe and the Middle East and their pathogenicity to Australian skeleton weed was studied.

Only very few samples collected in the western Mediterranean region were capable of infecting the intermediate- and broad-leaf forms of skeleton weed (Hasan 1972). The area of survey was therefore extended to more eastern Mediterranean countries. Here several strains were found to be virulent to the intermediate-leaf form. Among these, two strains (TU-21 from western Turkey and IT-36 from eastern Italy) have been demonstrated to be host-specific, and introduced into Australia where they have been released in the field for the biological control of their host form (Hasan 1981, 1984). Further search is under way to discover strains virulent on the broad-leaf form of *C. juncea*. Surveys in Greece and Turkey are part of this program.

Table 1. Pathogenicity of spore samples of *Puccinia chondrillina* Bub. & Syd. collected in Greece in May 1978 on the intermediate- and broad-leaf forms of *Chondrilla juncea* L.

Site		Pathogenecity			
		Intermediate-leaf form		Broad-leaf form	
		Plants with	Reaction	Plants with	Reaction
No.	Name	uredinia (%)	type[1]	uredinia (%)	type[1]
GR 4	Langadikia	0	1	0	0
GR 5	Thebes	1	3	0	1
GR 6	Athens	2	3	0	2
GR 7	Korinthos	0	2	0	1
GR 8	Neforika	0	0	0	0
GR 9	Chilimidion	0	1	0	1
GR 10	Spataloff	0	1	0	1
GR 11	Loutsa	0	1	0	1
GR 12	Chalkis	1	3	0	0
GR 13	Thessaloniki	0	1	0	0
GR 14	Lagadikia	0	1	0	0
GR 15	Asprovalta	0	2	0	1
GR 16	Xanthi	0	2	0	0
GR 17	Ferai	0	2	0	1

[1] Reaction type 0-5 (see text).

Materials and Methods

In Greece and Turkey, spores of *P. chondrillina* were sampled from a wide area, covering a diversity of climatic situations. To increase the possibilities of finding strains virulent against the broad-leaf form, two approaches were used: (1) seedlings of the three forms of Australian *Chondrilla* were exposed to the rust infection in the field amongst rusted skeleton weed populations; and (2) urediniospores of *P. chondrillina* were collected from a large number of sites in Greece and Turkey and brought to France to test their infectivity.

Spores were collected by a cyclone collector or on cotton swabs contained in glass vials, and stored at 5°C.

Plant inoculations were made according to Hasan (1981). The pathogenicity of the different spore samples to Australian forms of *C. juncea* was assessed by: (1) estimating uredinia and urediniospore numbers/unit area of the infected leaf; and (2) repeated microscopic examination of the cleared and stained leaf from the time of inoculation onward (Bruzzese and Hasan 1983) to follow the sequence of germ tube penetration and subsequent development of mycelium within the leaf tissue. Plants were also directly

Table 2. Pathogenicity of *Puccinia chondrillia* Bub. & Syd. sampled from Greek sites in autumn 1980 and spring 1981 and 1982 to the intermediate-and broad-leaf forms of Australian *Chondrilla juncea* L.

Site		Pathogenicity			
		Intermediate-leaf form		Broad-leaf form	
No.	Name	Plants with uredinia (%)	Reaction type[1]	Plants with uredinia (%)	Reaction type[1]
GR 20	Stylis	16	2-3	0	0
GR 24	Levadia	0	0	0	0
GR 25	Lefktra	14	3	0	0
GR 26	Thebes	0	0	0	0
GR 31	Keratea	100	5	100	4
GR 32	Pallini	60	4	0	1
GR 34	Plaka	100	4	20	3
GR 35	Pikermion	67	4	0	2
GR 36	Markopoulon	20	3	0	2
GR 37	Diastalrossis	0	2	0	0
GR 38	Rea	0	-	0	1
GR 39	Kapandriti	0	0	0	0
GR 40	Vravrona	0	2	0	0
GR 41	Amfiaro	0	1	0	1
GR 42	Stylis	100	3	0	1
GR 43	Levadia	100	4	0	1
GR 45a	Thebes	66	3	0	0
GR 45b	Thebes	66	4	0	0
GR 48	Aliartos	33	3	0	1
GR 49	Skydra	66	3	0	1
GR 50	Arnissa	0	-	0	1
GR 51	Florina	0	1	0	0
GR 52	Anixis	0	-	0	0
GR 53	Ionia	33	3	0	1
GR 54	Kompoti	33	3	0	0
GR 55	Serrai	66	4	0	1
GR 56	Iraklia	33	3	0	1
GR 57	Rodopolis	66	4	0	1
GR 58	Kilkis	66	4	0	0
GR 59	Thessaloniki	33	3	0	0
GR 59a	Thessaioniki	66	3	0	1
GR 60	Lankadikia	0	1	0	1
GR 61	Asprovalta	0	1	0	1
GR 62	Eleftheroupoulis	0	-	0	2
GR 63	Xerias	0	2	0	1
GR 64	Xanthi	66	3	0	0
GR 65	Polianthos	33	2	0	2
GR 66	Adriani	33	3	0	1
GR 67	Koropi	66	3	0	1
GR 68	Malakasa	33	4	0	1
GR 69	Lepoutra	100	4	0	1
GR 70	Krieza	33	3	0	1
GR 71	Eretria	100	4	0	1
GR 72	Psachna	0	2	0	2
GR 73	Pirgos	0	2	0	1
GR 74	Elec	0	2	0	2
GR 75	Gargaliani	33	3	0	0
GR 76	Pilos	0	-	0	0-1

Table 2. Continued.

Site		Pathogenicity			
		Intermediate-leaf form		Broad-leaf form	
No.	Name	Plants with uredinia (%)	Reaction type[1]	Plants with uredinia (%)	Reaction type[1]
GR 77	Rizomilos	0	2	0	0
GR 78	Kalamata	0	0	0	0
GR 79	Githion	0	1	0	0
GR 80	Karie	0	-	0	2
GR 81	Tripolis	33	3	0	1
GR 82	Napflion	0	2	0	2
GR 90	Neamanolada	25	3-4	0	1
GR 91	Manolas	20	3-4	0	0
GR 92	Krestena	0	1	0	1
GR 93	Megalopolis	50	4	0	1
GR 97	Neakoroni	0	2-3	0	0
GR 101	Areoplis	0	1	0	2
GR 103	Molai	0	1	0	0
GR 107	Karie	0	-	0	1-2
GR 108	Vlaherna	0	-	0	0
GR 109	Davia	0	-	0	0
GR 112	Astros	25	4	0	0
GR 113	Karnezeika	0	2-3	0	1
GR 114	Argos	0	1	0	2
GR 115	Chania	0	0	0	1
GR 117	Agii Deka	0	0	0	0
GR 119	Kapandriti	0	0-1	0	0-1
GR 120	Stayros	25	4	0	0
GR 40-121	Vravron	25	4	0	1
GR 36-122	Markopoulon	25	4	0	0
GR 124	Plaka	50	4	0	1
GR 125	Sikaminon	25	4	0	0
GR 126	Alepohori	25	4	0	0

[1] Reaction type 0-5 (see text).

examined for rust symptoms. Results of microscopic and macroscopic observations were used to grade a plant for increasing susceptibility on a modified 0–5 scale of reaction types already used for similar studies (Purdy and Allan 1963; Hasan 1972).

Results and Discussion

Selection of Puccinia chondrillina *Strains from Greece*

A preliminary survey was made in Greece in spring 1978 and spores of *P. chondrillina* were sampled from a restricted number of sites from central and northern Greece. Pathogenicity of these spore samples was tested on intermediate- and broad-leaf forms of Australian *C. juncea*. A few of these produced rust pustules on the intermediate-leaf form, but none was pathogenic to the broad-leaf form (Table 1).

More extensive surveys were undertaken in autumn 1980, and spring 1981 and 1982. Rust spores were collected from a wider area covering a diversity of climatic conditions from north of Thessaloniki to southern Peloponnesus and the island of Crete. A number of samples collected during these surveys produced symptoms on the intermediate-leaf

Table 3. Pathogenicity of the urediniospores of *Puccinia chondrillina* Bub. & Syd. sampled in Turkish sites in November 1981 and June 1980 and 1982 to the intermediate- and broad-leaf forms of *Chondrilla juncea* L.

Site			Pathogenicity			
			Intermediate-leaf form		Broad-leaf form	
No.		Name	Plants with uredinia (%)	Reaction type[1]	Plants with uredinia (%)	Reaction type[1]
TU	24	Cimsit	80	5	60	4
TU	25	Kulu	60	5	0	2
TU	26	Cihanbeyli	70	5	40	4
TU	28	Damlakuyu	100	5	100	4
TU	36	Kisla	0	0	0	1
TU	38	Icerijumra	20	4	0	0
TU	41	Kireli	30	4	0	1
TU	42	Kucuk	0	2	0	1
TU	44	Serik	20	4	0	2
TU	45	Antalya	0	2	0	2
TU	49	Selcuk	0	1	0	1
TU	52	Bostance	0	2	0	1
TU	57	Bursa	20	3	0	1
TU	62	Gulbaga	100	4	80	4
TU	63	Saray	0	2	20	3
TU	64a	Cubuk	33	4	0	1
TU	64b	Incesulu	33	4	0	2
TU	65	Sabanozu	100	4	0	1
TU	66	Ortaköy	100	4	0	2
TU	67	Elmadag	0	1	0	1
TU	68	Kirikkale	0	1	0	2
TU	69	Etimegut	33	4	0	1
TU	70	Golbasi I	60	4	33	4
TU	71	Golbasi II	60	4	12	4
TU	78	Karapinar	0	1	0	1
TU	79	Kargaci	0	1	0	1
TU	80	Eregli	100	4	0	2
TU	82	Ulukisla	0	0	0	1
TU	83	Pozanti	0	-	0	0
TU	84	Guzeloluk	0	-	0	2
TU	86	Alanya	0	0	0	2
TU	94	Sadiye	66	3	0	1
TU	95	Ergibayat	0	1	0	0
TU	96	Keslik	0	2	0	1
TU	97	Tausancali	0	1	0	1
TU	104	Ogulbeyi	100	4	0	1
TU	105	Kayas	100	4	33	4
TU	108	Ahiboz	75	4	0	2
TU	112	Karahamzali	75	4	0	0
TU	119	Tingir	0	0-1	0	0
TU	120	Sakyakan	0	2	16	3
TU	124	Gulek	50	4	16	3
TU	125	Kargicak	50	4	33	3-4
TU	126	Karaman	25	3	0	0
TU	127	Ayranci	25	3	16	3
TU	128	Degirmerburun	75	4	0	2
TU	129	Karasinir	25	4	0	2
TU	130	Icicumra	50	4	0	3
TU	131	Kadinhani	25	3-4	0	0

Table 3. Continued.

Site		Pathogenicity			
		Intermediate-leaf form		Broad-leaf form	
No.	Name	Plants with uredinia (%)	Reaction type[1]	Plants with uredinia (%)	Reaction type[1]
TU 132	Ilgin	25	3	0	2
TU 133	Aksehir	100	4	16	3
TU 134	Antalya	100	4	0	1
TU 135	Aksu	50	3	16	3
TU 136	Dag	75	4	16	3-4
TU 137a	Bucak	50	4	0	0
TU 137	Sav (Nahiye)	0	0	16	3
TU 139	Zivecik	50	4	0	2
TU 140	Yenice	25	4	0	3
TU 141	Aksaray	25	4	0	2
TU 142	Neusehir	0	0	0	2
TU 143	Kayseri	25	3	0	3
TU 144	Sarioglan	0	2	0	0
TU 145	Gemerek	50	4	0	2
TU 146	Sarkisla	0	1	33	3-4
TU 147	Bunyan	0	1-2	0	1
TU 148	Pinarbasi	0	1	0	0-1
TU 149	Orensehir	0	-	0	1
TU 150	Yemliha-Kasabasi	50	4	0	2
TU 151	Bogazliyan	0	0	0	0
TU 152	Yenikisla	0	0	0	0
TU 153	Divanlikoy	25	3-4	0	0
TU 154	Yozgat	25	4	0	3
TU 155	Delice	50	4	0	2
TU 156	Sungurlu	0	1-2	0	1-2
TU 158	Bogazkale	25	3-4	0	1
TU 159	Cicekdagi	0	0	0	0-1
TU 160	Cogun-Bakinevi	0	0-1	0	-
TU 161	Kirsehir	25	4	0	2
TU 163	Havaalani	100	4-5	0	0
TU 167	Eldivan	50	4	0	0
TU 168	Batikent	20	3-4	0	2
TU 169	Kizilcahamam	25	4	0	0
TU 170	Burak	100	4	0	2-3
TU 171	Gerede	100	4	0	2-3
TU 172	Eryaman	50	4	0	0
TU 173	Yenikent	0	0	20	3-4
TU 174	Beypazari	100	4	20	3-4

[1] Reaction type 0-5 (see text).

form while most of them did not infect broad-leaf skeleton weed. However, a few spore samples from southern Greece infected both forms but were only partially pathogenic to the broad-leaf form (Table 2). Amongst them, strain GR-31 was isolated from the site Keratea and was multiplied separately on intermediate- and broad-leaf forms.

The results of spore samples were similar to those obtained with the *C. juncea* seedlings exposed in the field during 1981. Only plants of broad-leaf form exposed at Keratea developed the rust pustules. Spores from these pustules were brought to the laboratory, and *C. juncea* plants inoculated by these developed symptoms similar to those inoculated by GR-31.

P. chondrillina *Strains from Turkey*

Field surveys in western Turkey began as early as 1978. Spores of *P. chondrillina* were collected from areas around Canakkale, Izmir and Istanbul. The strain TU-21 from Manisa near Izmir produced rust pustules on the intermediate-leaf form of Australian *C. juncea*. After this strain was shown to be host-specific it was introduced into Australia for the biological control of its host form (Hasan 1981).

In the following years the surveys were extended to central Turkey. Several spore samples collected in this region, especially areas near Ankara, gave both positive infections on intermediate-leaf form and also good development of mycelium in the leaves of the broad-leaf form, which was by then the main target form of skeleton weed for control. A more extensive search was made in the same areas, and several strains infecting only intermediate- or both intermediate- and broad-leaf forms have been discovered. Among these later strains TU-24, TU-26, TU-28, TU-62 and TU-105 have been found to be virulent to intermediate-leaf form (reaction type 4–5) but partially pathogenic to broad-leaf form (reaction type 4) (Table 3). Surveys in 1983 further eastwards and into northern Turkey have revealed the presence of several strains which similarly infect both intermediate- and broad-leaf forms. However, the search still continues for a strain strongly pathogenic to the broad-leaf form of *C. juncea*.

During surveys in summer 1983, in addition to spore collection, samples of skeleton weed seeds have been collected from individual plants from a large number of sites in Turkey and these seeds are at present under study for protein enzymes. The results of this study will be compared with the isozyme patterns produced by the Australian skeleton weed forms. This may confirm the presence in Turkey of the broad-leaf form and/or of skeleton weed forms closely similar to it. Further sampling of spores from the same areas should increase the probability of finding strains suitably virulent to the broad-leaf form of skeleton weed.

In the interim, strain TU-28 has been selected for host-specificity testing and this is now nearly complete. The results of testing and further observations on the behaviour of different strains from Turkey will be the subject of future publications.

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Biocontrol of Leafy Spurge with Pathogenic Fungi

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Abstract

Alternaria tenuissima f. sp. *euphorbiae* causes extensive leaf, stem and floral necrosis of leafy spurge, *Euphorbia esula*, a serious rangeland weed in northern U.S.A. and Canada. Natural infection is more common in protected areas than on open prairie, but seldom kills plants. Research is underway to enhance effectiveness of *A. tenuissima* f. sp. *euphorbiae* for possible use in biocontrol of leafy spurge. In greenhouse studies, inoculation with 5.5×10^5 conidia/ml in 0.5% Dupont WK wetting agent caused extensive stem infection and death of floral organs, and prevented seed set. However, growth of numerous new branches from axillary buds below the region of stem necrosis partially compensated for the tissue that is killed. Also, crown buds and roots are apparently not damaged by such infections. Field tests of the pathogen in two North Dakota and two Montana locations during summer 1984 were negative. Inoculations caused little or no necrosis and no reduction in biomass.

Powdery mildew, caused by *Microsphaera euphorbiae*, occurs late in the season and causes little discernable damage to infected plants. A rust fungus, *Uromyces striatus*, kills nearly all infected plants. However, it seldom occurs, its pycnial-aecial stages do not repeat, and its alternate host is alfalfa; consequently it holds little potential as a biocontrol agent. *Sclerotinia sclerotiorum* causes rapid wilting and death of leafy spurge, but its wide host range precludes its use. *Sclerotium rolfsii* provides similar results, but regrowth from crown buds leads to rapid recovery. *S. rolfsii* has an even wider host range on economically important plants than *S. sclerotiorum*. However, since it cannot overwinter in cold climates it would not become established in northern U.S.A. or Canada. Successful biocontrol of *E. esula* with pathogens remains an elusive goal at best.

Lutte Biologique Contre L'Euphorbe Ésule au Moyen de Champignons Pathogènes

Alternaria tenuissima f. sp. *euphorbiae* provoque une importante nécrose des feuilles, des tiges et des fleurs de l'euphorbe ésule, *Euphorbia esula*, une plant nuisible dans les pâturages du nord des États-Unis et au Canada. L'infection naturelle est plus courante dans les zones abritées que dans les prairies, mais les champignons sont rarement mortels. Des chercheurs tentent actuellement d'accroître l'efficacité de *A. tenuissima* f. sp. *euphorbiae* pour qu'elle puisse être utilisée dans la lutte biologique contre l'euphorbe ésule. Au cours des études en serre, l'inoculation avec 5.5×10^5 conidies par millilitre dans une solution de 0.5% de produits mouillants DuPont WK provoque une importante infection des tiges et la mort des organes floraux et empêche le développment des graines. Nous publions les résultats des essais d'inoculation effectués sur le terrain en 1984. Un champignon de la rouille, *Uromyces striatus*, tue presque tous les plants infectés. Toutefois, ce champignon est rare; il n'y a pas de répétition des stades de pycnidie et d'écidie et son autre hôte est la luzerne. Par conséquent, ce champignon offre peu de possibilités comme agent biologique. *Sclerotinia sclerotiorum* cause le flétrissement et la mort rapide de l'euphorbe ésule, mais cette espéce ne constitue pas un agent biologique appropriée compte tenu de la gamme de ses hôtes. *Sclerotium rolfsii* a des effets similaires, mais ne détruit pas les bourgeons de la couronne, ce qui permet à la plant nuisible de récupérer rapidement. Une lutte biologique efficace contre *E. esula* au moyen d'agents pathogènes n'est pas encore réalisable.

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Biological Control of *Cannabis sativa*

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Abstract

Fusarium wilt caused by *Fusarium oxysporum* f. sp. *cannabis* is a suitable pathogen for use in the biological control of unwanted *Cannabis sativa*. Inoculum appropriate for large scale field use can be grown on a variety of media. One gram/m^2 (8.8 lb/A) of prepared inoculum results in 50% mortality of susceptible *C. sativa* the first year and increases in succeeding crops. The fungus can be seedborne. Italian hemp cultivars are resistant to the disease while all other cultivars are susceptible. The fungus causes disease only in *C. sativa*. No other kinds of plants have been infected. Because of the restricted host range, no special precautions are necessary for controlled use of the fungus.

Lutte Biologique contre *Cannabis sativa*

La fusariose provoquée par *Fusarium oxysporum* f. sp. *cannabis* constitue un agent pathogène approprié pour la lutte biologique contre la plant nuisible *Cannabis sativa*. Un inoculum s'adaptant à l'utilisation à grande échelle peut être cultivé dans toutes sortes de milieux. Une préparation de 1 g/m^2 (8.8 lb/A) permet de tuer 50% des plants sensibles de *C. sativa* au cours de la première année et ce pourcentage augmente au cours des années ultérieures. Le champignon peut se développer dans les graines. Les cultivars de chanvre italien sont résistants à la maladie tandis que tous les autres cultivars sont vulnérables. Le champignon ne nuit qu'à *C. sativa*. Aucune autre espèce de plantes n'a été infectée. En raison de la gamme restreinte d'hôtes, aucune précaution particulière ne doit être prise pour contrôler l'utilisation du champignon.

Introduction

The purpose of this study was to determine the feasibility of using fusarium wilt, caused by *Fusarium oxysporum* Schlecht. f. sp. *cannabis* Noviello & Snyder (Hyphomycetes) to control unwanted *Cannabis sativa* L. (Moraceae). The objectives of the research were to determine: (1) the genetic stability and host specificity of *F. oxysporum* f. sp. *cannabis*; (2) methods of producing and applying inoculum; (3) effectiveness of the fungus in the field; (4) survival of the fungus in soil and reinfection of host plants in succeeding seasons; and (5) special precautions or techniques for controlled use of the fungus as a pathogen directed to disease production in a specific host.

Fusarium wilt of hemp (*C. sativa*) causes serious losses in the cultivated crop in Italy (Noviello and Snyder 1962). The disease was observed in a field at Alvignano, Caserta, in 1959 and in some other localities in 1960. The foliage of infected plants yellows, wilts, dries up and hangs on the plants. A dark-brown discoloration of the vascular system attends the foliage symptoms. As a rule, infected plants are killed. In the field, the disease is first noted in June when the plants are three months old, and by the end of June the disease is very evident. The disease is known to occur naturally only in Italy.

The disease is caused by *F. oxysporum* f. sp. *cannabis*. The form of the fungus that attacks *C. sativa* is highly specialized and is not known to infect other crop plants. *F. oxysporum* specialized forms are restricted in pathogenicity to very limited host ranges (Snyder and Hansen 1940). For example, the tomato form only attacks tomato. Crop plants such as watermelons, alfalfa, and beans (all susceptible to different specialized forms of the fungus) are not affected when grown in fields known to harbor the tomato form of the fungus, *F. oxysporum* Schl. f. sp. *lycopersici* (Sacc.) Snyder & Hansen. Hops (*Humulus lupulus* L.; Moraceae), one of the closest crop plants related to *Cannabis* spp., are not known to be susceptible to a fusarium wilt disease anywhere in the world.

Genetic Stability

The area devoted to the cultivation of hemp in Italy has declined from a high of 20,000 ha to the present level of approximately 80 ha in all of Italy. The crop is no longer grown in the Caserta area where fusarium wilt was severe in 1959. Most of the hemp in Italy is now grown in an area near Naples. The susceptible cultivars grown in 1959 and 1960 are no longer cultivated. The cultivar grown in 1972 through 1975 was 'Super Fibra' ('SF').

Hemp fields in Italy were visited in 1972, 1973, 1974 and 1975. Hemp plants exhibiting fusarium wilt were difficult to find but some infected plants were found and isolations were made from stem tissues. The fungus was present in most of the selected, infected plants. In 1972 the fungus was recovered from plants from three different fields. The incidence of the disease was very low; possibly $< 0.1\%$. *Sclerotium rolfsii* Sacc. (Agonomycetes), broomrape, and stem-boring insects made it difficult to identify plants with fusarium wilt. We now know that 'SF' is very resistant to fusarium wilt and this explains the low levels of the disease encountered. In retrospect it is surprising that it was even possible to find the disease.

The isolates of the fungus recovered from the hemp plants were similar in appearance on agar medium. Pathogenicity tests were conducted using four Italian hemp cultivars available: 'SF'; 'Carmagnola Originaria'; 'Eletta Campana'; and 'Carmagnola Selezionata' ('CS'). Roots of seedlings were planted in a sand-peat potting mixture and maintained in a growth chamber at 27°C. Very few plants exhibited fusarium wilt symptoms; however, the fungus was recovered from two plants of 'CS'. Twenty single-spore cultures were established from the re-isolated fungus. The single-spore isolates were all similar in appearance and did not differ from other isolates of the fungus. The characteristics of the fungus in culture were very stable. The fungus appears the same on agar medium today as it did when first isolated in 1972.

Pathogenicity tests using the four Italian hemp cultivars, 'Iowa' and 'Iran' did not reveal differences in pathogenicity among the fungus isolates; thus there appears to be a single race or pathotype of the fungus which is genetically stable.

Cultivar Susceptibility

Twenty-two *C. sativa* seed collections from different parts of the world were evaluated for disease susceptibility. We had determined that wounds were not necessary for infection and that plants became infected when seeds were sown in infested soil. The inoculum level was very high, in excess of 10,000 fungus propagules/g of soil. The tests were conducted in a growth chamber in continuous light and 8 h at 21°C and

16 h at 27°C. Seedlings emerged in 4–6 days depending upon the age and vigor of the seed. The first dead seedlings appeared 10–12 days after sowing the seed. Cultivars or seed collections from Mexico (three different collections), Pakistan, Turkey, Thailand, India, Nepal, South Africa, Czechoslovakia, Poland and Iran were all highly susceptible to the disease and in general there were no survivors or escapes in the growth chamber study. The four Italian hemp cultivars were resistant, and only 10–20% of the seedlings became infected. The survivors generally developed normally and were uninfected at the termination of the experiment. The fungus was consistently isolated from dead or diseased plants of the susceptible cultivars. Seeds obtained from Portugal were also resistant. Mr. Melisurgo of the Italian Hemp Growers Association believes that the Portugal seed is of Italian origin, that is grown in Italy and is most likely 'SF'.

Seeds from escaped hemp plants collected in Iowa ('Iowa') were intermediate in susceptibility. When 'Iowa', 'Iran' and 'SF' were compared, 100% of the 'Iran' plants were dead after 30 days, 70% of the 'Iowa' plants were dead, and 20% of the 'SF' plants were dead at the conclusion of the experiment. Fifty percent of the 'Iran' seedlings were dead in 14 days, while 19 days passed before 50% mortality occurred in the 'Iowa' seedlings. The 'SF' seedlings that died did so mostly (90%) in the first 20 days.

Host Specificity

A variety of plants were tested for susceptibility to the fungus. Seeds were either planted in heavily infested soil (excess of 20,000 propagules/g) or were transplanted into infested soil. Isolations were made from any plant that differed from the non-inoculated control plants. The fungus was never isolated from any plants other than *C. sativa* 'Iran' plants grown at the same time in infested soil. The 'Iran' plants always became infested. The plants were maintained in a greenhouse at 27°C. Tomatoes, cotton, and carnations were also grown in soil infested with their respective *F. oxysporum formae speciales* and became infected. Plants grown in infested soil are listed in Table 1.

No crop plants, including tobacco, tomato, bean, wheat, grape, alfalfa, corn, potato, and squash, grown in rotations with hemp in Italy have become infected by the fungus.

Inoculum Production

Various animal feeds (including alfalfa meal, almond hulls, rolled barley, sugar beet pulp, cottonseed meal, rolled milo, safflower meal, soybean oil meal, malted barley, and barley straw) were evaluated as culture media for production of inoculum. Alfalfa meal, soybean meal and cotton seed meal were superior to the other feeds in the numbers of chlamydospores and conidia produced. The superiority of these materials may be related to the high protein content. Since these materials tended to cake and the fungus did not grow well in the autoclaved medium, they were diluted with barley straw to facilitate aeration and separation.

The fungus was grown on medium composed of barley straw (*Hordeum vulgare* L.; Gramineae) and soybean meal (*Glycine max* [L.] Merr.; Leguminosae) from which the oil had been extracted. The barley straw was milled so that the largest pieces were 30 mm but most pieces were smaller. Soybean meal, 160 g, was mixed with 800 g of barley straw and 2-*l* of water. The mixture was thoroughly stirred and placed in large glass flasks plugged with cotton for sterilization. It was necessary to autoclave the medium twice to eliminate heat-resistant bacteria. The first autoclaving was at 121°C for 1 h followed in 24 h by the second autoclaving for 1 h at 132°C.

Table 1. Plants grown in soil infested with *Fusarium oxysporum f. sp. cannabis* Noviello & Snyder.

Scientific Name	Common Name	Cultivar
Abelmoschus esculentus (L.) Moench	okra	Clemson Spineless
Allium cepa L.	onion	Tulelake 401
A. sativum L.	garlic	"Safeway"
Anethum graveolens L.	dill	-
Apium graveolens L. var. dulce (Mill.) Pers.	celery	Fordhook
Arachis hypogaea L.	peanut	Jumbo Virginia
Asparagus officianalis L.	asparagus	UC72
Avena sativa L.	oats	Montezuma
Beta vulgaris L.	beet	Ruby Queen
B. vulgaris	sugar beet	F56
B. vulgaris var. *cicla* L.	chard	Ocelga
Brassica juncea (L.) Czern. & Coss.	mustard	Fordhook Fancy
B. oleracea L. var. *botrytis* L.	cauliflower	Early Snowball
B. oleracea L. var. *capitata* L.	cabbage	Wisc. Golden Acre
B. rapa L.	turnip	Purple Top
Callistephus chinensis (L.) Nees	aster	Burpeana
Capsicum frutescens L.	pepper	Burpee Tasty Hybrid
Carthamus tinctorius L.	safflower	Gila
Chrysanthemum morifolium Ramat.	chrysanthemum	Iceberg
Cicer arientinum L.	chickpea	-
Citrullus lanatus (Thunb.) Matsum. & Nakai	watermelon	Klondike
Cucumis melo L.	muskmelon	Burpee 199
C. sativus L.	cucumber	Ashley
Cucurbita pepo L.	zucchini	Italian Marrow
Daucus carota L.	carrot	Danvers Half Long
Dianthus caryophyllus L.	carnation	Red Scania
Eschscholzia californica Cham.	California poppy	-
Glycine max (L.) Merr.	soybean	Kanrich
Gossypium hirsutum L.	cotton	SJ-1
Helianthus annuus L.	sunflower	Mammoth
Hordeum vulgare L.	barley	Calif. Mariout
Humulus lupulus L.	hop	California
Ipomea batatas (L.) Lam.	sweet potato	-
Lactuca sativa L.	lettuce	Great Lakes
Linum usitatissimum L.	flax	New River
Lycopersicon esculentum Mill.	tomato	Bonny Best
Matthiola incana (L.) R. Br.	stock	-
Medicago sativa L.	alfalfa	Moopa
Morus alba L.	white mulberry	-
M. nigra L.	black mulberry	-
Oryza sativa L.	rice	Colora
Papaver rhoeas L.	corn poppy	-
P. somniferum L.	opium poppy	Iran
Phaseolus aureus Roxbg.	mungbean	Yuba
P. vulgaris L.	bean	Calif. Red Kidney
Pisum sativum L.	pea	Thomas Laxton
Raphanus sativus L.	radish	Scarlet Globe
Solanum melongena L.	eggplant	Early Beauty

Table 1. Continued.

Scientific Name	Common Name	Cultivar
S. tuberosum L.	potato	Russet Burbank
Sorghum bicolor (L.) Moench.	milo	Double Dwarf
Spinacia oleracea L.	spinach	America
Trifolium repens L.	white clover	-
Triticum aestivum L.	wheat	Pitic 62
Vicia sativa L.	vetch	Lana
V. faba L.	fava bean	-
Vigna unguiculata (L.) Walp.	cowpea	California 3
Zea mays L.	sweet corn	Golden Bantam
Zinnia elegans Jacq.	zinnia	Bodger

After cooling, the medium was inoculated using conidial suspensions obtained from cultures of the fungus grown on potato-dextrose agar. After 2–4 wks at 20–22°C the inoculum was removed from the flasks and dried for 5–7 days in a laboratory room at 20–22°C, r.h. 40–50%. After drying, the inoculum was broken up by hand, placed in polyethylene plastic bags and stored in the laboratory or in a freezer at −10°C. No attempt was made to maintain the inoculum in a sterile condition after removal from the culture flasks.

The inoculum was composed of particles of the straw and soybean meal colonized by the fungus — mycelium, conidia, and chlamydospores.

The inoculum used in the 1974 field trials in Portici, Italy, was 3–4 months old. No appreciable loss of viability has been detected in inoculum kept at 20–22°C for 1 yr or at −10°C, although one might expect a slow loss of viability of inoculum kept at 20–22°C. A more detailed report has been published (Hildebrand and McCain 1978).

Application of Inoculum

In greenhouse and growth chamber studies the prepared inoculum was incorporated into soil at various levels. The soil was moistened and left undisturbed for 2 wks. The number of propagules of the fungus/g of soil was determined by soil dilution plating (Nash and Snyder 1962). Three hundred propagules/g of soil were present when 0.025 g of inoculum was mixed with 1000 g of air-dry sandy loam soil, 2900 propagules/g at 0.050 g/1000 g soil; 11,300 propagules/g at 0.250 g/1000 g soil; 18,500 propagules/g at 0.500 g/1000 g soil; 67,000 propagules at 2.50 g/1000 g soil; and 95,000 propagules/g at 5.00 g/1000 g soil.

When susceptible 'Iran' was sown in soil containing different levels of the fungus, the time required for total kill of the seedlings was proportional to the inoculum level. At 7000 propagules/g of soil, 100% mortality was reached in 9 days; at 1400 propagules/g, 15 days elapsed before 100% mortality was reached; 22 days at 700 propagules/g; and 47 days at 70 propagules/g. At 7 propagules/g, 25% mortality occurred after 47 days (when the experiment was terminated).

Effectiveness of fungus in the field. In April 1974, four fields in Italy were inoculated using three levels of air-dry straw-soybean inoculum. The inoculum was distributed by hand and mixed into the top 10 cm of soil with a hoe to prevent loss by blowing and so that the hemp plants would be certain to make contact with the inoculum.

Ten g/m^2 were distributed in the plot at Vitulazio, Italy. The soil at Vitulazio is a loamy clay. The inoculated plot was seeded to 'CS' and 'SF'. No *Fusarium*-infected plants were observed at harvest in July in this field.

A field near Alvignano, Italy, was inoculated with 10 g/m^2 and seeded with 'SF' and seeds from 'Iran'. There was insufficient seed of 'Iran' to plant the Marcianise and Vitulazio fields in 1974. When final disease counts were made in August, 71% of the 'Iran' plants had died while only two plants of 'SF' in the inoculated plots were found infected. The surviving 'Iran' plants in the inoculated plots were 1.45 m in height while those in the non-inoculated control plots were 3.60 m in height. The surviving plants were probably infected but isolations were not made from these plants. Isolations confirmed that the dead or dying plants were infected by the fungus. By June 14, 29% of the 'Iran' plants had died. It was clear that the inoculum was effective and that 'SF' was highly resistant to the disease.

There were two inoculum experiments conducted at Portici, Italy, in 1974. One was in a field of fine sandy loam and the other in large ceramic pots containing the same field soil. Three levels of inoculum were applied: 1, 10 and 30 g/m^2. Three cultivars of hemp ('CS', 'SF' and 'Iran') were seeded on 20 April 1974. There were four replications, and diseased (dead) counts were made periodically and the infected (dead) plants removed to facilitate counting. Removal of the dead plants of course reduced inoculum for succeeding crops. The first infected plants were removed from the plots on 4 June. Final counts were made on 3 August. Dead 'Iran' plants for the three levels of inoculum (1, 10 and 30 g/m^2) were 50, 94.2 and 93.7%, respectively. No plants in the non-inoculated plots became infected. The level of disease in the Italian hemp cultivars 'CS' and 'SF' was low: only 4% of the 'CS' cultivar died in the plots receiving the highest inoculum level of 30 g/m^2 and 14% of the 'SF' variety died at this inoculum level.

'Iran' plants that did not die in the Portici field were stunted. Plants in the non-inoculated plots averaged 1.3 m in height; those in the 1 g/m^2 plots were 0.96 m, and 0.71 m in the 10 g/m^2 plots. When height measurements were made, there were insufficient plants to measure in the 30 g/m^2 plots. Results from the experiment in the ceramic pots were almost identical to the field trial.

Downy mildew, *Pseudoperonospora cannabina* Otth (Hoerner) (Peronosporales), was severe on 'Iran' cultivar and zineb fungicide was applied to control the disease. Downy mildew was not severe on the Italian hemp cultivars and did not require sprays which were, however, applied.

Survival of the fungus in soil. An experiment was conducted in a sandy loam field at the University of California San Joaquin Valley Agricultural Research and Extension Center at Parlier. Two levels of straw-soybean inoculum, 1 g/m^2 and 10 g/m^2, were incorporated into the top 7.5 cm of soil on 16 April 1974. A crop of corn was planted which was harvested in October. The inoculated plots were sampled periodically and the number of propagules of *F. oxysporum* f. sp. *cannabis* determined. *F. oxysporum* f. sp. *cannabis* was readily distinguishable from the native *F. oxysporum* present.

The average number of propagules in the inoculated plots declined from the initial levels of 1500/g of soil in the 1 g/m^2 plots and 90,000 g of soil in the 10 g/m^2 plots to a just detectable level (19 propagules/g) in the 1 g/m^2 plots and 250 propagules/g in the 10 g/m^2 plots 200 days after incorporation. Monitoring of the fungus level was discontinued in the 1 g/m^2 plots after 200 days. After 460 days the propagule level had declined to 40/g in the plots that had received 10 g/m^2 of the straw-soybean inoculum.

Barley was planted in the spring of 1975. *F. oxysporum* f. sp. *cannabis* in the inoculated plots increased in numbers in senescent barley roots along with other *F. oxysporum* forms, and then declined again as the soil became dry. The last propagule count was made in August 1975, 16 months after inoculation. The fungus was still detectable at 125 propagules/g of soil. Survival of the artificial, straw-soybean inoculum in the absence of host plants was adequate to ensure the presence of the fungus in the soil for at least one growing season.

The experimental work area was fumigated with methyl bromide gas beneath a polyethylene cover in November 1975. The fungus is most likely no longer present in this field.

Reinfection of host plants. Three of the same fields in Italy inoculated and planted with hemp in 1974 were replanted in 1975. The susceptible 'Iran' cultivar was planted in each field in addition to seeds which were purchased in Portugal.

In the Vitulazio field, where no disease was detected in the resistant Italian hemp cultivars in 1974, there was 6.2% fusarium wilt in the 'Iran' in late July 1974 and little or no disease in 'Portugal'. The fungus was able to survive or maintain itself on the resistant cultivars.

In the Marcianise field, where in 1974 there were scattered infections in the resistant Italian cultivars without correlation to inoculum level, there was severe disease in 'Iran' and the amount of disease (mortality) was correlated with the 1974 inoculum levels. The percent mortality in July 1975 in the 1 g/m^2, 10 g/m^2 and 30 g/m^2 rates of inoculum (applied in April 1974) were 36, 87 and 93%, respectively.

The ceramic containers were also replanted using 'Iran', 'Portugal' and 'SF' seeds. Percent of disease were: 97.5% for 'Iran', 5.9% for 'Portugal', and 3.9% for 'SF'. There was no infection in the noninoculated pots since there was no contamination of these pots from soil movement.

Seed-borne inoculum. Susceptible 'Iran' plants that became infected in field plots in Italy did not produce seed. However, in most fusarium wilt diseases viable seeds do not become infected, but the fungus contaminates the seed as bits of infected tissue mixed with the seed or as spores that cling to the seed.

To demonstrate that *F. oxysporum* f. sp. *cannabis* could also be seed-borne, moistened 'Iran' seeds were mixed with straw-soybean inoculum and large visible pieces of inoculum removed. The inoculated seed was indistinguishable from the non-inoculated seed. After air-drying the seeds were planted in pasteurized soil. Fifty percent of the inoculated seeds became infected and died within 30 days, when the experiment was terminated.

Safety of Inoculum

Inoculum composed of straw-soybean meal colonized by the fungus was tested for mycotoxins and mutagens. Chloroform extracts of the inoculum were injected into mice with no adverse effects. The chloroform extracts were also used in culture medium of bacteria strains sensitive to mutagens. These tests were conducted by Dr. Leonard Bjeldanes, Nutrutional Sciences, University of California, Berkeley. Professor Chester J. Mirocha, Department of Plant Pathology, University of Minnesota, analyzed a sample of inoculum and found no T-2 tricothecene toxin nor diacetoxyscirpenol.

Discussion

In absence of host plants *F. oxysporum* f. sp. *cannabis* slowly declines in the soil. A relatively healthy crop of *C. sativa* might be grown in a previously infested field after a number of years, possibly five or more, free of *C. sativa*. But the disease would build up again on succeeding crops. Where *C. sativa* is a weed in other crops, susceptible *C. sativa* plants would be eliminated. Although 'Iowa' (from escaped plants) was not as susceptible as 'Iran', it is not known if the surviving plants grown in inoculated soil were escapes or were genetically resistant. If they were genetically resistant, then the effectiveness of the fungus as a weed control agent would be diminished.

Since resistant cultivars are known, it would always be possible to grow *C. sativa* in areas where the fungus had been introduced. The presence of resistant cultivars might limit the length of time that the fungus would be useful in the control of illicit marijuana.

For biological control purposes, inoculum of the fungus could be introduced by air. It would not be necessary for complete coverage of a field since natural spread would occur by soil and plant debris movement and through the use of contaminated seed.

The biological control of *C. sativa* utilizing the fungus should be tested in fields where *C. sativa* is a weed and in fields where *C. sativa* is an illicit crop. The introduction of straw-soybean inoculum of the fungus by airplane would be considerably less expensive than overland travel and burning or otherwise disposing of the illicit crop. It would also have the advantage of not being necessary to return to the same area in succeeding years.

Downy mildew was severe on 'Iran' cultivar in the Italian field trials. This fungus might also be used in a biological control program, and might even be used together with *F. oxysporum* f. sp. *cannabis*. Hemp downy mildew is not known to infect other plants but cross-inoculation studies with hemp and hop downy mildew (*P. humuli*) should be conducted since hop downy mildew has been reported from *C. sativa*. Production of inoculum of *P. cannabina* would be difficult since it would be necessary to grow the parasite on *C. sativa* plants and the sporangia are not long-lived. Plantings of infected *C. sativa* might be maintained upwind of areas where illicit *C. sativa* is grown.

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A Proposal for a Standardized Scale of Attack and Its Application to Biocontrol Agents of Weeds in Laboratory Screening Tests

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Abstract

Biocontrol agents of weeds commonly accept a greater range of hosts in the laboratory than they do in nature. The problem of relating screening tests of pathogens to the field is discussed. The two parameters involved are the susceptibility of the test plant, for which a scale from 0 to 9 is suggested, and the distribution of the plant. The main plant distribution criteria considered are its density, whether it is sympatric or allopatric with the target weed and whether it is cultivated or native. Modifications of the reaction type scale for use against insects are suggested and two examples, a pathogen (*Puccinia jaceae*) and an insect (*Tingis ampliata*) are discussed in detail.

Proposition pour une Échelle Normalisée de Mesure des Dommages Infligés aux Plantes et son Application aux Agents de Lutte Biologique Contre les Plantes Nuisibles au Cours des Essais de Sélection en Laboratoire

D'ordinaire, les agents de lutte biologique contre les plantes nuisibles ont une plus vaste gamme d'hôtes en laboratoire que dans la nature. L'auteur traite de la difficulté de faire correspondre les essais de sélection des agents pathogènes aux conditions réelles. Les deux paramètres qui entrent en ligne de compte sont la vulnérabilité de la plant mise à l'épreuve, pour laquelle une échelle de côtes de 0 à 9 est proposée, et la répartition de la plante. En ce qui concerne ce dernier paramètre, les principaux facteurs sur lesquels se fonde le classement sont: la densité, la nature sympatrique ou allopatrique par rapport à la plante nuisible cible et s'il s'agit d'une cultivée ou indigène. L'auteur propose des modifications de l'échelle de réactions pour facilites son application aux insectes ravageurs et présente en détail deux examples, celui d'un agent pathogène (*Puccinia jaceae*) et celui d'un insecte (*Tingis ampliata*).

Introduction

The purpose of screening biocontrol agents is to demonstrate their host specificity and hence prove their safety for introduction into new areas for control of weeds. The criteria for selecting plant species on which a biocontrol agent should be tested, has been outlined in detail by Zwölfer and Harris (1971) and Wapshere (1974). The cost of screening insect biocontrol agents in Canada has averaged 1.1 scientist years (Harris 1979) or about $100,000. The cost for pathogens should be similar. An introduced biocontrol agent must inflict a certain amount of damage to the target weed to justify this cost. Thus, a method of recognizing effective agents before a screening program is started is important (Harris 1973). A major problem with the tests is that candidate agents frequently accept plant species in the laboratory that they do not in nature (Dunn 1978). Also there is a gradation in the susceptibility of the test plants which is not directly related to their risk of attack in nature. This paper proposes a scale to quantify the susceptibility of test plants to candidate biocontrol agents. In nature the hazard of a given level of susceptibility varies with the plant's density and range. Thus, interpretations are suggested for the various susceptibility ratings in relation to plant distribution. It is hoped that the scale will enable an effective and consistent assessment of a biocontrol agent. It is primarily directed toward plant pathogens, but can also be adapted to insect agents.

Reaction Scale

Disease ratings on a scale from 0 to 4, based on development and sporulation of each individual infection, have been used for cereal rusts since the turn of the century (Stakman and Levine 1922; Stakman *et al.* 1962) and later for mildews (Mains and Dietz 1930). Such ratings were used in differentiating formae speciales of rusts and mildews and in breeding for resistance to these pathogens in cereals. Field scales for estimating intensity of rust attack have also been developed (Peterson *et al.* 1948) based on the percent of leaf area covered with pustules and chlorotic areas on a scale from 0 to 100. Several modifications of these scales have later been adapted to other crops. James (1971) prepared a *Manual of Assessment Keys for Plant Diseases,* which covers most field crops, and gives good illustrations of percent of leaf and stem areas covered with symptoms. Based on this literature and practical experience a scale of reaction types from 0 to 9 was prepared (Table 1). The terms resistant, moderately resistant, moderately susceptible and susceptible, normally used in host-parasite relationships, were adopted giving each group two levels on the scale as well as 0 (to indicate total resistance) and 9 (to indicate high susceptibility). To quantify these reaction types, percent figures are given for each scale level (Table 1). Larger gradation in relation to percent was given at the resistant end of the scale, because slight variances there (especially when percent of test plants killed or yield loss is scored) are regarded more important than at the susceptible end of the scale.

Table 1. Scale of reaction types of plant species screened to biological control agents.

Reaction type	Percent damage
0. Totally resistant (immune)	0
1. Resistant	1-2
2. Resistant	3-5
3. Moderately resistant	6-8
4. Moderately resistant	9-12
5. Moderately susceptible	13-20
6. Moderately susceptible	21-35
7. Susceptible	36-50
8. Suceptible	51-70
9. Highly susceptible	71 and higher

The scoring system must be applicable for estimating effectiveness of the biocontrol agent on the target weed as well as potential damage to non-target plants. Thus, factors being scored vary according to type of organism being screened and information sought. Reaction types for pathogens can be grouped into three categories:

(1) *Proportion of test plant material covered with lesions.* Rusts, mildews and many leaf pathogens make local infections, and proportion of plant material covered with

pustules or lesions is proportional to damage inflicted on plants and ability of the pathogen to spread and survive.

(2) *Proportion of test plants killed.* Many pathogens infect plants locally in stems or roots, blocking water and nutrient transport (Sclerotinia wilt, Dutch elm disease, etc.) causing the entire plant to wilt and die.

(3) *Effect of attack in terms of yield loss in percent of normal host plant.* The potential of an agent to damage a given plant species can be rated as a percent of the damage done to its most susceptible host.

Application of Reaction Scale to Pathogens

To justify a screening program, a potential biocontrol agent must be in the susceptible range of the target weed.

In the ideal situation, all tested non-target plant species show total resistance in all growth stages to a biocontrol agent under laboratory conditions. Unfortunately, often a slight attack occurs. In the case where only the cotyledons are attacked, but not affecting seedling development severely, and true leaves are totally resistant, there should be little cause for concern, because it is unlikely that the organism would survive or cause any damage to such plant species under natural conditions.

Development of adult plant resistance to organisms pathogenic in the seedling stage, has been demonstrated in wheat to stem rust (DePauw 1974), stripe rust (Kuderling 1936), and in oats to crown rust (Harder *et al.* 1984). Susceptibility in the seedling stage normally is cause for concern. Therefore, plants to be screened should be tested with pathogens at the 4- to 6-leaf stage. However, depending on the type of plant species attacked and the organism involved, further tests on mature plants and under natural conditions might be warranted.

In the field, damage to non-target plant species by a biocontrol agent will depend on whether the plants are common or rare and whether they are sympatric or allopatric to the main host plants of the organism. These factors have to be taken into consideration when results of screening tests carried out in the laboratory, are analyzed.

The term sympatric means that species occur together in the same geographical area, *vs.* allopatric, where species occur in different geographical areas as shown in Fig. 1. The geographical areas in the northern half of the continent have been modified from those used in the *National List of Scientific Plant Names* (USDA 1982) to follow vegetation zones rather than political boundaries.

A summary of proposed guidelines for interpretation of reaction types in relation to non-target plants is given in Table 2. Field crop plants are genetically homogeneous within a cultivar and are grown in monocultures. This gives ample possibilities for selection and development of pathogenic strains of an organism. Therefore, any organism that can survive and develop on a field crop under natural conditions, whether allopatric or sympatric, is not acceptable for introduction. However, there should be no cause for concern if only abortive infections (reaction type 1–2) occur and no significant effect on crop plants are detected on 4–5 cultivars of the crop with 2–3 isolates of the organism under laboratory conditions. A reaction type 3 (moderately resistant) on a sympatric field crop would require field tests conducted in the area of origin to prove that the organism cannot survive or develop on such crops under field conditions. In allopatric field crops, for which chances of exposure to the organism is remote, reaction types 1 and 2 are acceptable, but thorough laboratory tests are needed for reaction type 3, and field tests in area of origin is required for reaction type 4. If the scoring indicates the proportion of test plants killed by the organism, a reaction type 1 requires field tests for sympatric field crops and a reaction type 2 (up to 5% of test plants killed) is not acceptable, as indicated in Table 2.

Sympatric common economic native plant species (e.g. important for honey production) and common ornamentals could be at risk at a reaction type 4, and thus would require testing of 4–5 different sources of the plants to 2–3 different isolates of the agent to assure that no significant damage could occur. Non-economic native plants with a type 4 reaction would be of less concern, because they are native and, therefore, likely heterogeneous and thus damage to the plant population would be limited. Also, some pressure from consumers (organisms) would not be of any consequence on non-economic plant species (Harris 1982). A reaction type 5 or more on common non-weedy native plants and common ornamentals that are grown in large plantings is not acceptable.

Table 2. Interpretation of reaction types of non-target plants tested with potential biocontrol agents under laboratory conditions.

Reaction Type[1] (Table 1)	Type of non-target plant species tested	Acceptability of tested biocontrol agents for release
0 (Immune)	All	Acceptable
1-2 (a)	All wild plants and ornamentals	Acceptable
	Sympatric field crops	Test 4-5 cultivars to 2-3 different strains of agent, acceptable if stable and not causing significant damage.
3 (a), 1 (b)	All wild plants and ornamentals	Acceptable
	Allopatric field crops	Test 4-5 cultivars to 2-3 different strains of agent, acceptable if stable and not causing significant damage.
	Sympatric field crops	Will require further field tests in area of origin to prove that agent cannot survive or develop on crop under field conditions before acceptance for release.
4 (a), 2 (b)	Non-economic wild plants and uncommon ornamentals	Acceptable
	Sympatric economic wild plants and common ornamentals	Test 4-5 sources of seed to 2-3 different strains of agent, acceptable if stable and not causing significant damage.
	Allopatric field crops	Will require further field tests in area of origin to prove that agent cannot survive or develop on crop under conditions before acceptance for release.
	Sympatric field crops	Not acceptable
5-9 (a), 3-9 (b)	Allopatric, scattered rare wild plants and uncommon ornamentals (not grown in large plantings)	Acceptable
	Field crops, sympatric wild plants and common ornamentals (grown in larger plantings)	Not acceptable

[1] a = scoring indicates proportion of plant area covered with lesions; b = indicates proportion of test plants killed. (See catagory 1 and 2 under reaction scale).

Rare or endangered native plants occurring sympatrically with the target weed would be at risk if they are moderately susceptible (reaction type 5) to the biocontrol agent regardless of whether they occur scattered or in clumps (dense stands). On the other hand, rare, allopatric, scattered native plants are not at risk, even though fully susceptible, because the chance of the organism reaching such a plant species would be small. Should they be attacked, they would be damaged, but the organism would have little chance of reaching another susceptible plant. However, rare plant species occurring in clumps, although allopatric, are more at risk (if attacked by the organism) because they have a better chance of becoming established. The chance of an organism reaching such allopatric plant species depends on geographical barriers, prevailing winds and the type of organism involved. Winged insects and many rust spores can readily be picked up and carried over large distances by wind in contrast to many root- and stem-rot pathogens, which produce more mucoid spores and, therefore, do not spread as readily. In the case of wind-borne organisms with no geographical barriers present, native plant species that are moderately susceptible (reaction type 5 or more) could be at risk even though the distance between the target weed and the native plant species is large.

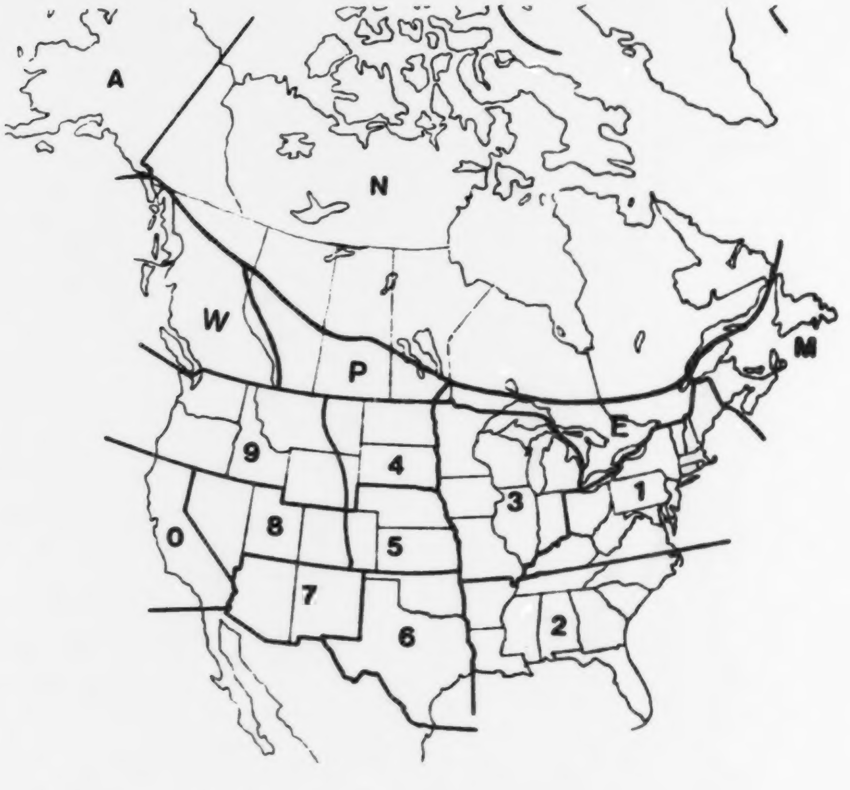

Fig. 1. Geographical areas of plant zones in North America. (Modified from U.S.D.A. 1982.)

On uncommon ornamentals not normally grown in large plantings, a moderately susceptible reaction type 5 to 6 is acceptable because the chance for the organism to reach them and establish itself is small. When the appearance of an ornamental is important, less visual damage can be accepted, but ornamentals not grown in large plantings could be protected with pesticides at a relatively low cost and, therefore, a higher susceptibility level to a potential biocontrol agent might be acceptable.

Application of Reaction Scale to Insects

The reaction scale proposed in Table 1, although designed for pathogens, is general enough to be applied to insects also. The factors being scored would be somewhat different. The first category described for pathogens can be divided into two categories when applied to insects:

(1) *The amount of plant material consumed directly by an insect.* Many leaf-feeding insects (flea beetles, caterpillars, etc.) are defoliators, thus the actual amount of plant material consumed is a good measure of the stress inflicted on the plant, similar to grazing pressure by livestock in pastures.

(2) *Percent development, survival and reproduction rate of an insect.* The amount of plant material consumed may not be proportional to the survival and reproduction rate of an insect. If an insect can complete its life cycle on a plant species, that indicates that the nutrient content of the plant satisfies the needs of the insect and thus could be a suitable host.

(3) *Proportion of test plants killed.* This category (category 2 for pathogens) can be directly applied to insects such as root- and stem-boring insects, where nutrient transport to the rest of the plant is cut off, resulting in wilting of the entire plant.

(4) *Effect of attack in terms of yield loss in percent of normal host plant.* This category (category 3 for pathogens) can also be directly applied to insects. Gall-forming insects (including many seed flies) cause abnormal growth of plant tissue, resulting in a sink which restricts the development of normal tissue that severely stunts plants or reduces seed production. Sucking insects like aphids and mites also drain plant tissue for nutrients, likewise resulting in stunting and less vigor of attacked plants.

The interpretation of laboratory tests for insects would be similar to pathogens described above. Since insects can actively search for host plants in nature, in contrast to pathogens that are restricted to the plants they accidentally land on, the preference of plants under natural conditions becomes very important in interpretation of laboratory screening tests, as discussed by Dunn (1978).

In feeding tests the flea beetle *Altica carduorum* Guerin-Méneville (Coleoptera: Chrysomelidae) fed and survived well on its main host, *Cirsium arvense* (L.) Scopoli and *C. palustre* (L.) Scop. (Compositae). The pupation rate of first instar larvae was slightly lower on *C. palustre* (70%) as on *C. arvense* (80%). The amount of leaf area eaten in seven days by adult beetles was 22% higher on *C. palustre* than on the main host *C. arvense* (Harris 1964). This could indicate that *C. palustre* is less nutritive and thus a larger amount is required than when feeding on the main host. Therefore, although *C. palustre* appears to be a suitable host to *A. carduorum* in a starvation test, it is less preferable, because larger amounts are required. Perhaps this is the reason that *A. carduorum* has not been observed on *C. palustre* in Europe.

Discussion

A European knapweed rust (*Puccinia jaceae* Otth.; Uredinales), collected in Eastern Europe (Watson *et al.* 1981), was screened for potential biocontrol of diffuse knapweed (*Centaurea diffusa* Lam.; Compositae), which is a serious weed of rangeland in British Columbia (Watson and Renney 1974; Harris and Cranston 1979). In screening tests this rust was found to infect safflower with fully susceptible pustules on cotyledons, but on true leaves more resistant type pustules occurred (Watson and Alkhoury 1981) with infection type 1–2+ on the rust infection scale (Stakman *et al.* 1962) which would equal a reaction type 3 in the proposed scale in Table 1. In a test, where knapweed rust was inoculated on safflower plants in the 4–6 leaf stage (cotyledons in good condition) and in the bolting stage just prior to flowering, a slight yield reduction in dry matter compared to controls was found 42 days after inoculation. A 7% loss was detected when inoculated at the 4–6 leaf stage and a 3% loss in the bolting stage (Mortensen 1985). A 7% yield loss would, according to Table 1, also result in a reaction type 3. According to Table 2, a reaction type 3 on a sympatric field crop would require further field tests of the agent on such a crop in the area of origin, before final decision is made. Presently tests are being conducted in Europe.

In screening tests, *Tingis ampliata* H.-S. (Hemiptera: Tingidae), a potential biocontrol agent for Canada thistle, *C. arvense*, was found to survive and lay eggs on globe artichoke (*Cynara scolymus* L.; Compositae) and safflower (*Carthamus tinctorius* L.; Compositae) although at a much lower frequency than on Canada thistle (only 9.7 and 0.2% respectively, of the eggs laid on Canada thistle). The survival of first instar nymphs was 22% on globe artichoke compared to 88% on Canada thistle. None of the nymphs tested on safflower survived (Peschken 1977). On the scale in Table 1, globe artichoke would be rated reaction type 4–6 depending on the characters scored for. Safflower would be rated reaction type 1–2, because adult tingids can survive, but the nymphs were not capable of developing. According to Table 2, a reaction type 1–2 on safflower, a sympatric field crop, would be acceptable if stable and not damaging field crops significantly. The globe artichoke, with a reaction type 4, which is allopatric or marginally sympatric with Canada thistle, would require field tests in Europe. The susceptibility of globe artichoke is thus on the borderline of acceptance, and the author recommended that it should not be released in Canada at the present time, but should other released biocontrol agents fail to control Canada thistle the case might be reconsidered.

These are two examples of biocontrol agents, a pathogen and an insect, that both showed slight attack on a field crop in screening tests. According to proposed scale and interpretation, field tests in area of origin to prove or disprove that the agent can survive or damage the crop in nature, were required in both situations. In one case the researcher recommended not to release the agent; in the other, further field tests are being conducted before a final decision is made. The proposed scale and its interpretation were intended to initiate establishment of set rules and guidelines which could be followed for screening exotic biocontrol agents of weeds and their approval for release. This would make the job easier and more concise for both researchers and for reviewers dealing with approval of release.

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Colletotrichum coccodes, a Mycoherbicide for Velvetleaf*

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Abstract

Velvetleaf (*Abutilon theophrasti*) is a major weed of soybean and corn in North America which is not adequately controlled by presently available technology. A fungus, *Colletotrichum coccodes*, was isolated from blighted velvetleaf leaves in Vermont. Abundant spores were produced in liquid culture which were used in laboratory and field experiments. In controlled environment studies, the disease developed on velvetleaf over a broad range of environmental conditions. Warmer temperatures (24 *vs.* 18°C) and longer dew periods (24 *vs.* 12 h) favoured disease development. A spore concentration of 10^7 spores/ml produced high levels of disease and leaves of seedlings to the 12-leaf stage were susceptible to the pathogen. In field trials with *C. coccodes*, velvetleaf was effectively controlled in soybeans with an application of 10^9 spores/m^2.

Colletotrichum coccodes, un Mycoherbicide Contre l'Abutilon

L'abutilon (*Abutilon theophrasti*) est une plant nuisible importante d'Amérique du Nord que l'on retrouve dans les cultures de mais et de soja. Les méthodes actuelles de répression se sont avérées inefficaces contre cette plant nuisible. Un champignon, *Colletotrichum coccodes*, a été isolé à partir de certaines feuilles d'abutilon trouvées au Vermont et montrant des symptômes de brûlure. Une quantité abondante de spores a été produite en culture liquide afin de réaliser des essais en laboratoire et aux champs. Des expériences sous conditions contrôlées ont démontré que la maladie pouvait se développer sous une large gamme de conditions environnementales. Des températures plus élevés (24°C *vs.* 18°C) et une période d'humidité plus longue (24 h *vs.* 12 h) ont favorisé de développement de la maladie. Une concentration de 10^7 spores per millilitre produit des tauz élevés de maladie. Les plants d'abutilon étaient susceptibles depuis le stade de plantule jusqu'au stade de 12 feuilles. Des essais aux champs avec *C. coccodes* ont démontré que l'abutilon croissant dans des cultures de soja peut être efficacement réprimé par une application de 10^9 spores au metre carré.

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Host Range of the Haplontic Phase of *Uromyces rumicis*

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Abstract

Teliospores of *Uromyces rumicis* produced on detached dock leaves, could be activated to germinate by storing the spores for 60 days on water agar at 2°C in continuous darkness. Within 10 days, after changing the teliospores to 8°C under light, up to approximately 70% of the teliospores germinated with basidia and basidiospores. *Ranunculus Ficaria* was the only species that could be infected by the basidiospores (haplontic phase) of *U. rumicis*. Eleven species of the genus *Ranunculus*, 16 other species out of the family Ranunculaceae, 12 crop plants, *Rumex crispus*, *R. obtusifolius* and *Berberis vulgaris* could not be infected. Lack of knowledge about the host range of the haplontic phase of *U. rumicis* is no more a prevention of biological control of *Rumex* weeds with this rust fungus.

L'Éventail de Plantes-Hôtes de la Phase Haplontique d'*Uromyces rumicis*

Des téliospores d'*Uromyces rumicis*, élevés sur des feuilles detachées de patience (*Rumex patientia*), et tenus sur le gel d'agar a 2°C, dans l'obscurité totale, ont pu être activées à la germination. A moins de 10 jours d'un changement de conditions (8°C, et lumière), 70% environ des téliospores avaient germiné, avec des basidia et des basidiospores. Le *Ranunculus ficaria* était la seule espèce pouvant être infectée par les basidiospores (phase haplontique) d'*U. rumicis*. Onze espèces du genre *Ranunculus*, 16 autres espèces de la famille Ranunculacées, 12 plantes vivières, *Rumex crispus*, *R. obtusifolius* et *Berberis vulgaris* n'ont pu être infectées. Le manque de connaissance concernant l'éventaibl des hôtes d'*U. rumicis* n'empêche plus son emploi dans le biocontrôle des *Rumex* nuisibles.

Introduction

In 1967, the U.S. Department of Agriculture began to study the potential of *Uromyces rumicis* (Schum.) Wint. (Uredinales) as a biological control agent against *Rumex crispus* L. (curly dock; Polygonaceae). *R. crispus* is a common weed in the United States and in other regions of the world.

U. rumicis is a macrocyclic heteroecious rust fungus. In the dicaryotic phase it infects species of the subgenus *Lapathum* within the genus *Rumex* (Gäumann 1959; Inman 1971). This subgenus includes common weeds like *R. crispus*, *R. obtusifolius* L., and *R. pulcher* L. Besides this subgenus, Morris (1982) described the fungus on *Emex australis* Steinh. (Polygonaceae) in South Africa. The risk of infecting economic plants in the dicaryotic phase is presumed by Inman (1971) as sufficiently low.

Less is known concerning the host range of the haplontic phase of *U. rumicis*. Tranzschel (1905, 1909) and Gäumann (1931) described *Ranunculus Ficaria* L. (Ranunculaceae) as the only alternate host of *U. rumicis*. Inman (1971) was unsuccessful in confirming these results, because of inability of teliospores to germinate.

The rust is presumed to be absent from the United States and is not listed by Arthur and Cummins (1962) as occurring in the country (cit. in Inman 1971). The sufficient potential of the rust in controlling curly dock was demonstrated by Inman (1971). Nevertheless a release of the fungus in the United States was prevented, because of a failure in testing the host range of the haplontic phase of *U. rumicis* (Frank 1973).

The purpose of this paper is to present a method to activate teliospore germination under controlled conditions and to test several selected species of plants for susceptibility to *U. rumicis* in the haplontic phase.

Table 1. List of crops plants, other plants and Ranunculaceae (except genus *Ranunuculus*) tested.

Species	Cultivar	Notes[1]
Crop plants		
Triticum aestivum L.	Kolibri	b
	Probus	b
Zea mays L.	Orla 312	b
	LG 11	b
Beta vulgaris L.	Kawemono	d
Spinacia oleracea L.	Monapa	a
Medicago sativa L.		e
Phaseolus vulgaris L.	Top crop	a
Pisum sativum L.	Eldo	a
Trifolium pratense L.		e
T. repens L.		e
Nicotiana tabacum L.	Sota 50	c
Solanum lycopersicum L.	Montfavet	a
Cucumis sativus L.	Chin. Schlange	a
Ranunculaceae		
Aconitum compactum Rchb.		f *
Anemone blanda Sch. et K.	Pink Star	a *
A. coronaria L.	de Caen	a *
A. pulsatilla L.	Küchenschelle	a
Aquilegia alpina L.	alpine Columbine blue	a
A. hybrida L.	Koralle lachsrot	a *
Caltha palustris L.		f *
Clematis Muraski	Deep purple	a *
Delphinium ajacis L.	Kalsey	a
D. cultorum Voss.	Stand up	a *
D. grandiflorum L.	Chinese	a
D. zalil (*sulphureum*) Aitch. et Hensl.	Rittersporn	a
Eranthis hiemalis (L.) Salisb.	Winterling	a *
Nigella damascena L.	Miss Jeckyll	a
Thalictrum dipterocarpum Franch.	purpurlila	a *
Trollius europaeus L.	Globe Flower	a *
Other Plants		
Berberis vulgaris L.		f
Rumex crispus L.		f *
R. obtusifolius L.		f *

[1] * = Species tested in the climatic chamber and in the field experiment; a = Samen Mauser, Zurich, Switzerland; b = UFA Samen, Winterthur, Switzerland; c = Sota, Changins, Switzerland; d = Kleinwanzlebner Saatzucht, Kleinwanzleben, Western Germany; e = Landwirtschaftliche Forschungsanstalt, Reckenholz Zurich; and f = collected in Switzerland by us.

Materials and Methods

Rust and Plant Materials

Uredospores of *U. rumicis* were collected in Switzerland: in Männedorf (R-113) on *R. crispus* and in Mols (R-35) on *R. obtusifolius*. Both strains were collected by the authors and propagated in the greenhouse on their original hosts. Plant material used is listed in Tables 1 and 2. Plants were either collected by us or obtained (see Tables 1 and 2) and were grown in sterilized soil (Potgrond Topferde, de Baat, Netherlands) in clay pots (diam. 12 cm) in the greenhouse (16 h light at 20°C, 8 h dark at 15°C, 60% r.h.).

Table 2. List of species of the genus *Ranunculus* tested.

Species	Origin	Notes[1]
R. aconitifolius L.	Wängialp, Switzerland	*
R. alpestris L.	Frutt, Switzerland	a
R. arvensis L.	Jaca, Spain	d
R. auricomus L. *s.l.*	Affoltern, Switzerland	*
R. californicus Benth.	USA	c
R. Ficaria L.	Männedorf, Switzerland	
	Grüningen, Switzerland	*
	Luzern, Switzerland	*
R. flammula L.	Emmen, Switzerland	a
R. Friesianus Jordan	Klöntalersee, Switzerland	
	Bern, Switzerland	*
R. gramineus L.	Switzerland	a
R. millefolius Banks & Sol.	Greece	a
R. repens L.	Zurich, Switzerland	*
Ranunculus sp.	commercial seed	b *

[1] * = species tested in the climatic chamber and in the field experiment. Seeds or plants obtained by: a = garden center "Alpengarten Eschmann", Emmen Switzerland; b = Samen Mauser, Zurich, Switzerland; c = University of California, Santa Barbara, USA; d = Botanical Garden of Basel, Switzerland. All other *Ranunculus* species were collected by the authors.

Method to Activate Germination of Teliospores

Teliospores were produced on detached leaves of *R. obtusifolius*. Young leaves were cut, inoculated with a uredospore suspension and put in a pot filled with Perlit® (granular mineral of quartz expanded by heating) and tap water. Leaves were covered with a plastic bag and put in a chamber at 8°C. Artificial illumination was given for 12 h (Philips, TL 20W/55, 1500–2500 lux). Approximately 35–45 days after inoculation the teliospores, formed on the detached leaves, were suspended in water. The suspension was passed through a hydrophilic cellulose nitrate filter (Sartorius 8 μ, diam. 5 cm; Gold and Mendgen 1983). The filter with the thin spore layer was put into one petri dish containing 2% water agar (Bacto-Agar, Difco).

In experiment A, teliospores in petri dishes were incubated at different temperatures (2, 8, 15, 21°C) under artificial illumination (12 h) or in continuous dark. Every 10 days the percent of germinated teliospores was determined (10 × 100 teliospores were scored) microscopically in each treatment. A teliospore was considered to be germinated if the germ tube (the basidium) was at least longer than the spore.

In experiment B, teliospores were stored for 60 days at 2°C in continuous dark. After this storage, spores on filters were changed to different temperatures (2, 8, 15, 21°C). Artificial illumination was given for 12 h. Percent of germinated teliospores was determined 10 days later, as described above.

Experiments A and B were done with R-35. For each treatment, three petri dishes were used. Every experiment was repeated at least three times.

Results of germination tests were analysed using Duncan test at the level $P < 0.05$.

Inoculation Experiment

Teliospores were produced and put on cellulose nitrate filters as described above. Spores were then stored 60 days at 2°C in the dark. After that treatment they were suspended in water and sprayed on the different test plants (Tables 1 and 2). At the moment of inoculation all plants were in a young, growing stage. Plants were placed for 2 wks in a plastic chamber (12 h light at 12°C, 12 h dark at 10°C, 100% r.h.). After removing the plastic, r.h. was dropped to 80%.

All *Ranunculus* species were inoculated separately with each strain (R-35 and R-113). Other species were inoculated with a mixture of the two strains. All inoculation experiments were done with at least five plants/species or ecotype and were repeated three times. Infection severity was checked one and two months after inoculation.

Field Experiment

During three years, different species of Ranunculaceae (see Tables 1 and 2) were growing together with *R. crispus* and *R. obtusifolius* in a field plot (10 m^2). Alternately a row of *Rumex* plants were arranged next to a row of Ranunculaceae plants. At least four plants of each species of Ranunculaceae were used. Each summer the docks were inoculated with uredospores of different strains. In spring, plants were checked for aecia.

Results

Teliospore Formation

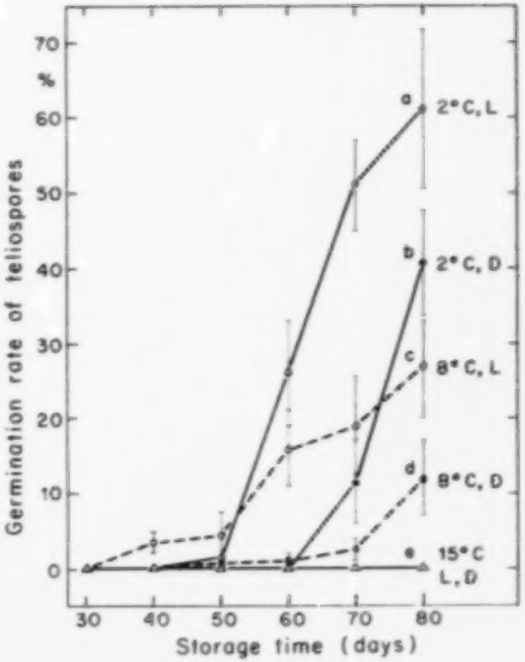
Teliospore formation occurred 20–25 days following inoculation of the detached dock leaves with uredospores. Rust strain R-35 produced approximately 80% teliospores, and strain R-113 up to 40–50% teliospores (the rest were uredospores).

Teliospore Germination

Teliospores collected in nature or in the greenhouse germinated after winter storage outdoors. In spring (March to April), basidia and basidiospores were observed.

Teliospores, produced on detached leaves, germinated with basidia and basidiospores after relatively short storage on filters on water agar. In experiment A (Fig. 1) the best germination rate of teliospores was observed during an incubation at 2°C under light. They began to germinate abundantly after 50 days. Thirty days later up to 60% had germinated. At the same temperature but in continuous dark, beginning of germination was 10 days later, and germination rate remained less at any time. An incubation at 8°C under light or in continuous darkness had also a smaller effect on germination. During incubation at 15 or 21°C under light or in continuous dark the teliospores did not germinate.

In experiment B (Fig. 2), germination rate of teliospores stored for 60 days at 2°C in continuous dark, could be increased by incubating spores at 8 or 15°C under light.



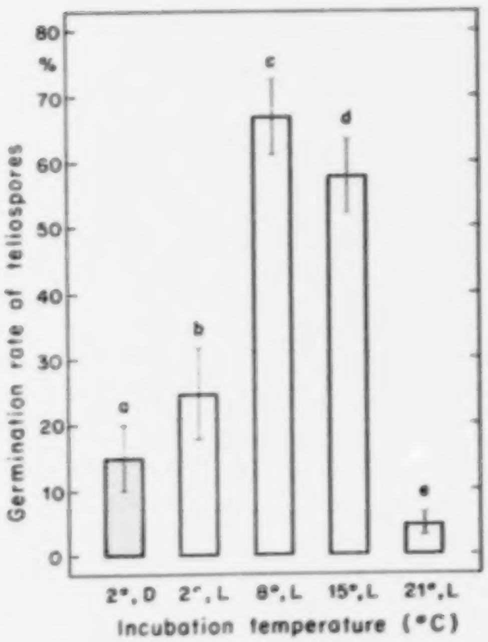


Fig. 1. (Left) Experiment A: Effect of incubation at different temperatures under light or in continuous darkness on germination rate of teliospores of *Uromyces rumicis* (Schum.) Wint. Points with a different letter are significantly different ($P < 0.05$). D = continuous darkness, L = 12 h light.

Fig. 2. (Right) Experiment B: Effect of different temperatures on germination rate of teliospores of *Uromyces rumicis* (Schum.) Wint. stored for 60 days at 2°C in the dark. Germination rate was determined after 10 days of incubation. Columns with a different letter are significantly different ($P < 0.05$). D = continuous darkness, L = 12 h light.

Within 10 days at 8°C up to approximately 70% of teliospores germinated; a similar effect was achieved at 15°C. Remaining at 2°C in continuous dark, or incubating at 2 or 21°C under light, had less effect on the germination rate.

Teliospores of rust strains R-35 and R-113, used for the inoculation experiment, both germinated up to 70%.

Host Range Test

R. Ficaria is the only host of the haplontic phase of the two strains of *U. rumicis*. Both in field experiments and in the climatic chamber aecia were produced only on this species.

In the climatic chamber the first pycnia were observed 2 wks after inoculation; three weeks later aecia with aeciospores appeared. In the field experiment aecia were observed in April. In every experiment a reinfection of *R. obtusifolius* with the aeciospores was successful.

No other plants showed any symptoms (necrotic or red spots) after inoculation, either in the climatic chamber or in the field experiment. Eleven species of the genus *Ranunculus*, 16 other Ranunculaceae species, 12 crop plants, *R. crispus*, *R. obtusifolius* and *Berberis vulgaris* L. (Berberidaceae) were tested (Tables 1 and 2). Some of these species were tested only in the climatic chamber (Tables 1 and 2).

A complete cycle from teliospores to teliospores (on detached dock leaves and *R. Ficaria* plants) required appraximately 130 days.

Discussion

Teliospores of *U. rumicis* germinate in nature after overwintering (Gäumann 1931). With the method described in this paper it is possible to activate germination of teliospores under controlled conditions in a relatively short time (60 days). The method allows inoculation of test plants at a temperature convenient to the plants at the beginning of germination.

The activation of teliospore germination by storing teliospores on water agar agrees with results of Groth *et al.* (1978) and Gold and Mendgen (1983) for bean rust teliospores. The break of dormancy is probably due to aging and following rehydration of the spores.

The results of the host range presented in this paper confirmed the work of Tranzschel (1905, 1909) and Gäumann (1931). Tranzschel reported for the first time the connection between the rust *U. rumicis* on docks and an aecidium on *R. Ficaria*. Gäumann observed that aecia were induced only on *R. Ficaria* after a natural overwintering together with leaves bearing telia of *U. rumicis*. *R. Stevenii* auct. non Andrz. (= *Friesianus* Jordan) and *R. bulbosus* L. were not infected. Attempts by Inman (1971) to induce pycnial and aecial infections by inoculations with teliospores were unsuccessful.

Frank (1973) suggests that *U. rumicis* overwinters, at least in the Rome area, mainly as uredia or vegetative mycelia on the primary host. Primary infection in spring is by uredospores, rather than aeciospores from the alternate host. This fact can increase the chance of successful biological control. The earlier in spring that uredospores appear, the better the possibility of control of docks.

Our studies have confirmed the high degree of specialization of *U. rumicis* in the haplontic phase. The lack of knowledge concerning the alternate host of the rust fungus was the only reason to prevent release of the organism for biological control of docks (Frank 1973). Our work has filled this gap and release is now possible.

Acknowledgments

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Biological Control of Hamakua Pa-Makani with *Cercosporella* sp. in Hawaii

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Abstract

A Jamaican foliar pathogen of *Ageratina riparia*, incorrectly named *Cercosporella* sp., was introduced into Hawaii on 10 November 1974. Extensive host range terrarium studies under quarantine in 1975 showed this pathogen to be highly host-specific and a safe biological candidate for Hamakua pa-makani control. Permission for its release was granted soon thereafter by the State of Hawaii Board of Agriculture. Host infection occurred at 10–20°C, and $>98\%$ r.h.; 18°C was optimal for infection, disease development and sporulation. Temperatures above 20°C were lethal to the pathogen. The disease is characterized by circular, light chlorotic specks developing into distinct dark to reddish-brown angular lesions with chlorotic margins on the upper leaf surface and massive white sporulation on the lower surface. The pathogen does not grow in normal laboratory media, characteristic of obligate parasites. Inoculum becomes airborne at night when r.h. is $>98\%$; spore distribution is accomplished by wind and rain. Devastating disease epidemics occurred in dense stands of *A. riparia* in cool, high rainfall sites of Oahu, Hawaii, and Maui, 2–3 months after pathogen release. Weed populations were reduced 80% to $<5\%$ in a 9-month period. Similar reduction in weed populations were recorded 3–4 yrs after pathogen release at sites with adequate moisture but temperatures above or below the optimal for disease development. Sites with low temperatures and low rainfall showed $>50\%$ reduction in weed population after 8 yrs of pathogen release. In general, more than 50,000 ha of pasture land have been rehabilitated to their full potential by this pathogen, while no evidence of host resistance nor the presence of mutants pathogenic to other plant species has been encountered in the 8 yrs since its release.

Le Biocontrôle de 'Hamakua Pa-Makani' à Hawaii, au Moyen d'une Espèce de *Cercosporella*

On a introduit à Hawaii, le 10 novembre, 1974, un agent pathogène des feuilles d'*Ageratina riparia*, *Cercosporella* sp., mal identifié d'abord, et originaire de Jamaïque. En 1975, des études poussées de l'éventail d'hôtes de cet agent, sous conditions de quarantaine, ont indiqué une haute specificité, de sorte que celui-ci promet d'être un agent sûr pour le contrôle biologique de 'Hamakua Pa-makani'. Peu après, le State of Hawaii Board of Agriculture a autorisé l'élargissement de cet agent pathogène. L'infection des hôtes s'est produite à des temperatures variant de 10° à 20°C, et à plus de 98% r.h., 18°C étant la temperature optimale pour l'infection, le développement de la maladie, et la sporulation. Des temperatures au dessus de 20°C se sont relevées mortelles pour l'agent pathogène concerné. La maladie est caracterisée par des tâches chlorotiques, claires et circulaires, qui se développent en lesions angulaires bien marquées, de couleur foncée ou brun-roux avec des marges chlorotiques, sur le dessus des feuilles et, sur la surface inférieure, une sporulation blanche et massive. L'agent pathogène ne se cultive pas dans les milieux ordinaires de laboratoire, ce qui est caracteristique de tout parasite obligatoire. Les spores se dispersent dans l'air, à l'aide du vent et de la pluie, lorsque l'humidité relative dépasse 98%. Entre 2 et 3 mois après l'élargissement de l'agent pathogène, des colonies d'*A. riparia* de haute densité dans des régions fraiches et très pluvieuses des îles d'Oahu, d'Hawaii et de Maui, ont été ravagés des épidemies de la maladie. Durant une période de neuf mois, les populations de l'herbe nuisible se sont rétrécies de 80% à plus de 95%. On a signalé des réductions semblables, 3 à 4 années après l'élargissement de l'agent pathogène, dans des endroits à humdité suffisante, mais où les temperatures étaient plus elevées ou moins elevées que l'optimum pour le développement de la maladie. Dans des endroits frais et peu pluvieux on a observé < 50% de réductions dans les populations d'herbes après 8 années d'élargissement de l'agent pathogène. En général, plus de 50,000 ha de pâturage ont été completement réhabilités au moyen de cet agent pathogène, au cours des 8 années suivant son élargissement, sans rencontrer ni de résistance de la part des hôtes, ni de presence de mutants nuisibles à d'autres plantes.

Introduction

Ageratina riparia K. & R. (= *Eupatorium riparium* Regel; Compositae), commonly known as Hamakua pa-manaki, was introduced to Hawaii around 1925 (Neal 1965). This member of the Compositae was originally collected from a canyon in El Mirador, Veracruz, Mexico, and taken to Germany by Linden in 1857. From here the plant was spread to other countries as an ornamental (Degener 1946). The species, outside of its range of origin, is a vigorous, hardy plant and prolific seeder; on its native habitat, Hamakua pa-makani could be considered an endangered species (E.E. Trujillo, unpubl. data). Its tiny papose seeds are readily wind disseminated and in moist, cool environments (e.g. forest floor and upcountry grazing lands of the Hawaiian islands), seeds germinate readily and the seedlings, free of natural enemies, grow profusely, dominating in time the natural vegetation covering forest floor and open grazing land (Hosaka *et al.* 1954). In 1973 it was estimated that more than 62,500 ha on the island of Hawaii were infested with this weed (H. Nako, pers. comm.). The infestation was concentrated largely in the Kau-Kona districts from 400–1800 m elevation. In Oahu, the infestation was serious in more than 10,000 ha of the Koolau Range from 300–900 m elevation. The weed also was present on the island of Maui on the Hana highway. In 1973 and 1974 two introduced phytophagous insects, a plume moth *Oidaematophorus* sp. (Lepidoptera: Pterophoridae) and a gall fly *Procecidochares alani* Steyskal (Diptera: Tephritidae), were released by the State of Hawaii Department of Agriculture (DOA) as biological control agents for this plant (Gardner and Davis 1979). The first was collected on *Ageratina pazcuarense* H. & R. (= *Eupatorium pazcuarense* Spregel) in the vicinity of Mexico city and the second on *A. riparia* at finca Mirador, in Veracruz, Mexico (W. Rose, pers. comm.).

A short presentation by the author of the biological control program of *Cassia surattensis* Lamarck (Leguminosae) with *Cephalosporium* sp. (Hyphomycetes) (Trujillo and Obrero 1978) to the Hawaii Cattlemen Council on 10 April 1973, motivated the support of the industry and a grant was received from the Barbara Cox Anthony Foundation to survey Mexico and the Caribbean area for plant pathogens of Hamakua pa-makani. This marked the first organized effort in Hawaii to utilize exotic plant pathogens for the control of weeds. Previously they had been ignored (Templeton and Trujillo 1981).

Methods and Materials

Two land explorations were conducted in Mexico. The first during July to August 1973 covering central Mexico from the U.S. border to Veracruz, and the second during November 1974 covering the Fortin-Jalapa area of Veracruz. The introduction of the pathogen *Cercosporella* sp. (Hyphomycetes) from Jamaica was by permission of Hawaii's Quarantine Section, DOA, and the Federal Animal and Plant Health Inspection Service (APHIS). The original introduction was done by hand-carrying living, diseased host material from Jamaica to Hawaii. Branches of diseased plants were collected before sunrise in the Blue Mountains, placed in a plastic bag, within a double plastic bag containing ice to keep the specimen at low temperature to ensure pathogen survival during the trip. Five leaves with sporulating lesions remained on the branches at arrival in Hawaii 48 h later. These served as the initial inoculum to inoculate four Hamakua and four Maui pa-makani (*A. adenophora* [Spreng.] R. & H.) plants growing in 51 cm (20-inch) diam. terrariums (Lawnware Products, 8220 N. Austin, Morton Grove, IL 60053), kept at a quarantine laboratory at Manoa. Inoculation was done by wetting with a fine brush the underside of the leaves with a spore suspension of the pathogen. Plants in terrariums at 100% r.h. were incubated at 18°C in an air-conditioned room under fluorescent illumination of *c.* 2700 lux.

Inoculum for subsequent studies derived from the original Jamaica inoculum, was maintained on *A. riparia* plants inoculated weekly with a spore suspension containing *c.* 200,000 spores/ml and incubated in terrariums at the environmental conditions previously stated. Inoculum was prepared by washing spores from 14-day-old inoculated leaves into a glass beaker and adjusting to the desired spore concentration with tap water using a spore counting chamber (Howard 1922). Similar inoculum concentrations were utilized for other studies.

All host range studies were conducted in Lawnware No. 340 espherical terrariums (51 cm [20 inches] in diam.). Humidity was adjusted through the manually operated opening at the top. The r.h. was maintained at 100% by adding a liter of water to the floor of the terrarium and closing the top; 98% r.h. was obtained by opening the ventilation window at the top about 2 cm. A battery operated psychrometer manufactured by Environmental Tectonics Corporation was used to measure r.h. Rooted, potted plants of different species tested were inoculated in sets of 4, while 4 Hamakua pa-makani plants inoculated with the same inoculum served as controls. Both leaf surfaces were wetted with tap water spore suspensions of the pathogen using a camel-hair brush. Inoculated plants were incubated at approximately 100% r.h. and 18°C for 24 h, and approximately 98% r.h. and 18°C for 14 days. Fifteen days after inoculation, disease incidence was recorded for inoculated test plants and Hamakua pa-makani controls. Detached *A. riparia* leaves inoculated and incubated at different temperatures in 150 mm diam. disposable petri plates containing a water-soaked paper towel, were used to determine effect of temperature on infection, disease development and sporulation.

Field inoculations were done initially by wetting the leaf surfaces of 100 randomly selected leaves with a camel-hair brush dipped in a spore suspension prepared as previously stated. Sites were selected at different elevations to provide the range of temperatures and humidities necessary for epidemics to occur. Subsequent field inoculations were done by spraying on the host the desired spore suspension with 500 ml plastic spray bottles. Disease was assessed by randomly collecting 10 diseased branches from a 30 m transect of the inoculated area, recording the total number of necrotic diseased leaves over the total number of branch leaves, expressing this as disease percent.

Results and Discussion

Exploration

Mexico's land exploration during July–August 1973 covered more than 10,000 km of roads from the U.S. border to Veracruz. The native plant habitat was located at the end of August in two canyons between Jalapa and Fortin, Veracruz. The specimens found at the time were free of plant pathogens or insect pests. Subsequently the gall fly *P. alani* was collected in this area by William Rose, exploratory entomologist with DOA, and shipped to Honolulu for further studies.

A rust affecting *A. riparia* was discovered in El Mirador, Veracruz, Mexico, in November 1974; however, because of insufficient biological information, this pathogen was not introduced to Hawaii. Explorations conducted in Jamaica during November–December of the same year were successful in finding a previously reported *Cercosporella* sp., the cause of leaf spotting of *A. riparia* in this Caribbean country (Leather 1967). This disease is characterized by circular, light chlorotic specks, to distinct dark reddish-brown, angular lesions with chlorotic margins, on the upper leaf surface (Fig. 1-A). Initial lesions on the lower leaf surface are small, circular to angular, pale green to whitish specks that later become woolly white in appearance, as masses of hyaline *Cercosporella* type nonseptate conidia form (Fig. 1-B). The nonseptate character of the conidia places the pathogen in a genus other than *Cercosporella*. Spores are produced on single hyaline conidiophores arising from hyaline sporodochia. As the spots enlarge, the center becomes necrotic and reddish-brown in color, while sporulation continues on the lesion margin, forming a white ring of spore masses (Fig. 1-C). As the disease progresses, spots become black and coalesce, and leaves necrotize and die. Preliminary pathogen biological information developed during the author's stay at the University of the West Indies, showed fungal characteristics of an obligate parasite. Isolation attempts on common media failed. The pathogen required low temperatures for spore germination on water agar (WA), V8 juice agar (V8) and Difco potato dextrose agar (PDA), where it germinated readily at 10, 14, 16 and 18°C. Although germ tube development occurred at these temperatures, no mycelium was produced or colonies developed. Spore germination ceased at temperatures higher than 20°C.

Field data gathered during exploration of the Blue Mountains and the northeastern coast of Jamaica pointed to a high pathogen specificity, none of the major crops examined nor representative species of more than 20 families of plants growing adjacent to diseased *A. riparia* showed evidence of white spore masses on the lower leaf surface, characteristic signs of the pathogen. As a result, the original introduction of the pathogen from Jamaica to Hawaii was done in living plant material.

Host Range Studies

The first visible symptoms on Hamakua pa-makani plants inoculated with the original Jamaica inoculum and incubated in terrariums at 18°C under incident illumination > 2700 lux appeared 9 days after inoculation. These showed as small, chlorotic specks on the upper leaf surface, becoming necrotic 12–13 days after inoculation. On the lower leaf surface the first visible signs of the pathogen appeared 7 days after inoculation as pinpoint, whitish protuberances immediately below the stomata. Microscopic examination showed these to be hyaline sporodochia filling the substomatal chamber. Subsequently, sporulation occurred abundantly, and by the 11th day the lesions on the underside of the leaves were covered with the characteristic white spore masses. No lesions developed on *A. adenophora*-inoculated plants; repeated pathogenicity tests gave similar negative results.

A. riparia was the only host found for *Cercosporella* sp. Inoculation tests on 40 plant species representing 29 families were all negative, while inoculated *A. riparia* controls always were positive. Inoculations involved: ti, *Cordyline terminalis* (L.) Kunth (Agavaceae); mango, *Mangifera indica* L. (Anacardiaceae); plumeria, *Plumeria obtusa* L. (Apocynaceae); anthurium, *Anthurium andraenum* Lind. (Araceae); pineapple, *Ananas comosus* (L.) Merr. (Bromeliaceae); papaya, *Carica papaya* L. (Caricaceae); beet, *Beta vulgaris* L. (Chenopodiaceae); calendula, *Calendula* sp., mums, *Chrysanthemun* sp., Maui pa-makani, *A. adenophora*, lettuce, *Lactuca sativa* L., ligularia, *Ligularia*

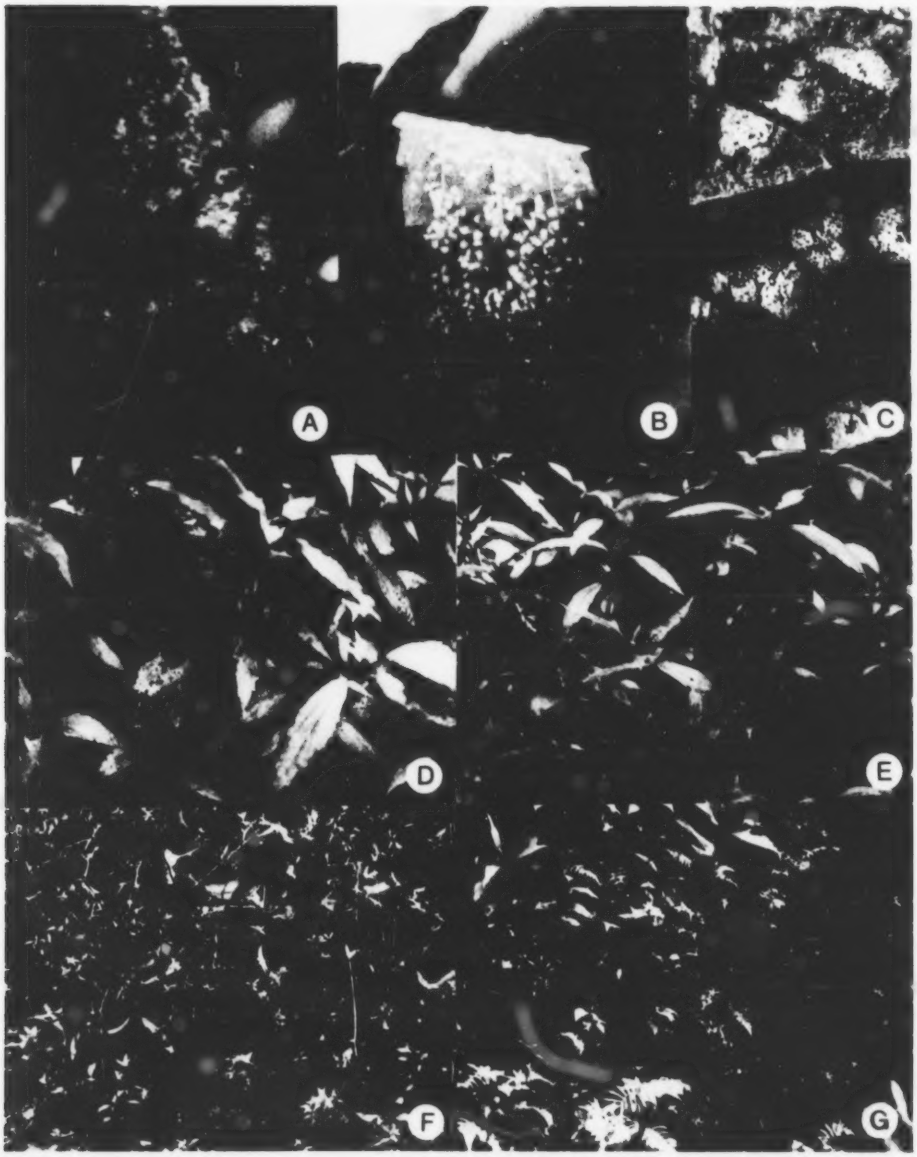

Fig. 1. '*Cercosporella*' blight of Hamakua pa-makani. (A) *Ageratina riparia* K. & R. upper leaf surface showing initial and advance symptoms of the disease. (B) Lower leaf surface showing white spore masses, sign of the pathogen. (C) Lower leaf surface showing initial and advanced necrotic spots magnified 8×. (D–G) Effects of disease epidemics on weed at Tantalus, Oahu, 1975–76, where ideal conditions for these prevailed: (D) 6 wks; (E) 10 wks; (F) 4 months; and (G) 6 months after pathogen release.

tussilaginea (Burm. f.) Makino, marigold, *Tagetes* sp., wedelia, *Wedelia trilobata* (L.) Hitchc. (Compositae); sweet potato, *Ipomoea batatas* (L.) Lam., morning glory, *Ipomoea* sp. (Convolvulaceae); head cabbage, *Brassica oleracea capitata* L. (Cruciferae); cucumber, *Cucumis sativus* L. (Curcurbitaceae); poinsettia, *Eurphorbia pulcherrima* Willd. (Euphorbiaceae); bamboo, *Bambusa* sp., sugar cane, *Saccharum officinarum* L. (Varieties 37–1933, 54–775 and Hawaiian purple), maize, *Zea mays* L. (Graminae); coleus, *Coleus blumei* Benth. (Labiatae); avocado, *Persea americana* Mill. (Lauraceae); beans, *Phaseolus vulgaris* L. (Leguminosae); hibiscus, *Hibiscus* sp. (Malvaceae); banana, *Musa* sp. (Musaceae); ohia lehua, *Metrosideros collina* (Fort.) Gray subsp. *polymorpha* (Gaud.) Rock., guava, *Psidium guajava* L. (Myrtaceae); dendrobium, *Dendrobium* sp. (Orchidaceae); coconut, *Cocos nucifera* L. (Palmaceae); lilikoi, *Passiflora edulis* Sims (Passifloraceae); phlox, *Phlox* sp. (Polemoniaceae); macadamia, *Macadamia ternifolia* F. Muell. (Proteaceae); rose, *Rosa* sp. (Rosaceae); coffee, *Coffea arabica* L., gardenia, *Gardenia jasminoides* Ellis (Rubiaceae); lime, *Citrus* sp. (Rutaceae); litchi, *Litchi chinensis* Sonn. (Spindaceae); snap dragon, *Antirrhinum* sp., (Scrophulariaceae); tomato, *Lycopersicon esculentum* Mill., egg plant, *Solanum melongena* L. (Solanaceae); lantana, *Lantana camara* L., jamaica vervain, *Stachytarpheta jamaicensis* (L.) Vahl. (Verbenaceae).

Optimal Temperature for Epidemics

Inoculation studies conducted on detached leaves in moist chambers at 100% r.h. and 10, 12, 14, 16, 18, 20 and 22°C showed 18°C as the optimal temperature for spore germination, infection, sporodochial formation, sporulation and symptom development. Spore germination and infection occurred from 10–20°C; no spore germination or infection occurred at temperatures higher than 20°C. Inoculation of detached pa-makani leaves by wetting the lower surface with *c.* 0.1 ml suspension containing *c.* 20,000 spores and incubated at 10, 12, 14, 16, 18, 20 and 22°C, and 100% r.h. for 20 days showed an average of 4, 13, 120, 220, 652, 198 and 0 lesions/leaves. At 18°C sporodochia was visible in 7 days and abundant sporulation occurred in 10–11 days after inoculation. At 10 and 12°C, sporodochial development was very slow, becoming visible with whitish protuberances on the leaf lower surface after 20 and 16 days, and white spore masses became visible in 30 and 20 days after inoculation, respectively. At incubation temperatures of 14, 16, 18 and 20°C, sporodochia formed and sporulation was observed 11, 9, 7 and 9 days after inoculation, and white spore masses became visible at 13, 12, 8 and 10 days, respectively. No infection occurred at 22°C as spores on the surface of the leaves failed to germinate. Microscopic observation of Acid fuchsin stained epidermal strips from inoculated leaves showed only ungerminated spores.

Spores subjected to temperatures higher than 24°C lost viability rapidly as temperature increased. Nine sets of three detached diseased leaves exhibiting more than 200 sporulating lesions were incubated at temperatures of 24, 28 and 32°C for 1, 5 and 24 h periods. Spores were removed from the lesions with a wet camel-hair brush and inoculated on nine sets of three healthy leaves and incubated for 18°C and 100% r.h. for 10 days. Spores survived 5 h at 24°C without noticeable loss in viability, as shown by the equal number of lesions formed on inoculated leaves by spores treated for 1 and 5 h to this temperature, while a 50% drop in viability was recorded for spores treated for 24 h; there was a 50% drop in the number of lesions produced by spores subjected to this treatment. Spores survived temperatures of 28–32°C for 1 h without appreciable loss in viability. Longer treatment times reduced viability significantly.

Effect of temperature on pathogen sporulation on host tissues was measured on detached diseased Hamakua pa-makani leaves. These were thoroughly washed with tap water and a camel-hair brush to remove spores present and dried with absorbent paper before incubating for 24 h at 14, 16, 18, 20 and 22°C and 100% r.h. Sporulation was abundant at 18, reduced by about one half at 16 and 20, hardly detectable at 14, and absent at 24°C. Attempts to determine the inoculum potential necessary to cause infection were made by inoculating a known spore concentration to the undersurface of 20 detached leaves incubated at 16°C. Lesions were counted 15 days after inoculation. The results of this experiment showed an inoculum potential of 70 spores/lesion.

Field Release and Biological Control Potential

In October 1975, the Hawaii Board of Agriculture, DOA, granted permission for field release of the *Cercosporella* sp. introduced from Jamaica as a biological control agent for Hamakua pa-makani. On 4 November 1973, plants were inoculated at three sites on the Tantalus Ridge of Oahu, at elevations of 450, 500 and 550 m. An initial inventory of the pa-makani population showed these sites to be 80% covered with the weed. In each site the leaves of 100 plants were wetted with a spore suspension containing *c.* 200,000 spores/ml. Lesions were visible 12 days after inoculation at 450 and 500 m elevation, and at 550 m 11 days after inoculation. Evidence of secondary infections were recorded at all sites 20 days after inoculation by the appearance of new lesions on a few non-inoculated leaves. Twenty-day-old lesions at all sites were about 2 mm in diam. and could be recognized by the necrotic centers already present, while secondary lesions showed as very small white specks. Sporulation was sparse at 450 m where temperatures were too high for the pathogen, while it was abundant at 500–550 m elevations with favorable temperatures.

No evidence of severe disease epidemic was recorded during the first 6 wks after inoculation in a 100 m radius around the inoculated site. However, after exploring the 9 km trail that goes from the western side of the Tantalus road to Pauoa flats and the ridge summit at 670 m elevation, evidence of extensive disease spread was recorded. During the first 300 m of trail no evidence of disease spread was noticed. The first evidence of disease was recorded about 550 m away from the inoculation site, where less than 1% of the foliage had small necrotic lesions; sporulation was massive on the underside of the lesion and some evidence of secondary infection was evident in some leaves. Approximately 1.6 km from the inoculation site and 600 m elevation, the first area with more than 5% diseased leaves was encountered. The greatest disease incidence was found at 650 m elevation, 4 km from the initial inoculation sites, where more than 10% of the leaves showed necrotic lesions. The rainfall at this elevation averages 7.112 m annually with temperature of 16°C at night, ideal conditions for epidemics of the disease to develop. A day after this finding, the St. Louis ridge, located 5 km to the northeast of Tantalus was surveyed. The disease was recorded at about 550 m elevation rather extensively distributed among the weed population of this uninoculated area. Subsequently, airborne spores of the pathogen were trapped on Rotorod air samplers (manufactured by Ted Brown Associates, 26338 Esperanza Dr., Los Altos Hills, CA 94022), used on Tantalus at 1.5 m from the ground from 7–7:30 pm when r.h. was > 95%. No spores were trapped in air sampled from 8:00 a.m. to 6:30 p.m., when r.h. was < 95%. The rapid spread of the pathogen in the area was possibly due to the normal air movement in Tantalus, typically downdraft in the evening and updraft early in the morning. A tropical storm which affected Oahu during 22–27 November 1975, with high winds and more than 300 mm of rain, provided optimal conditions for pathogen distribution and disease. The minimal-maximal temperatures for Tantalus during December were 12–24°C, ideal for infection and sporulation.

Monthly assessments of weed population at the initial Hamakua pa-makani inoculation sites at Tantalus showed a rapid decrease in foliage and plant vigor at all sites and the weed population dropped from 70–80% to < 1% in 9 months. In August 1976, most of the space once occupied by the weed was covered in other plant species such as ferns, grasses and indigenous plants (Fig. 1, D–G).

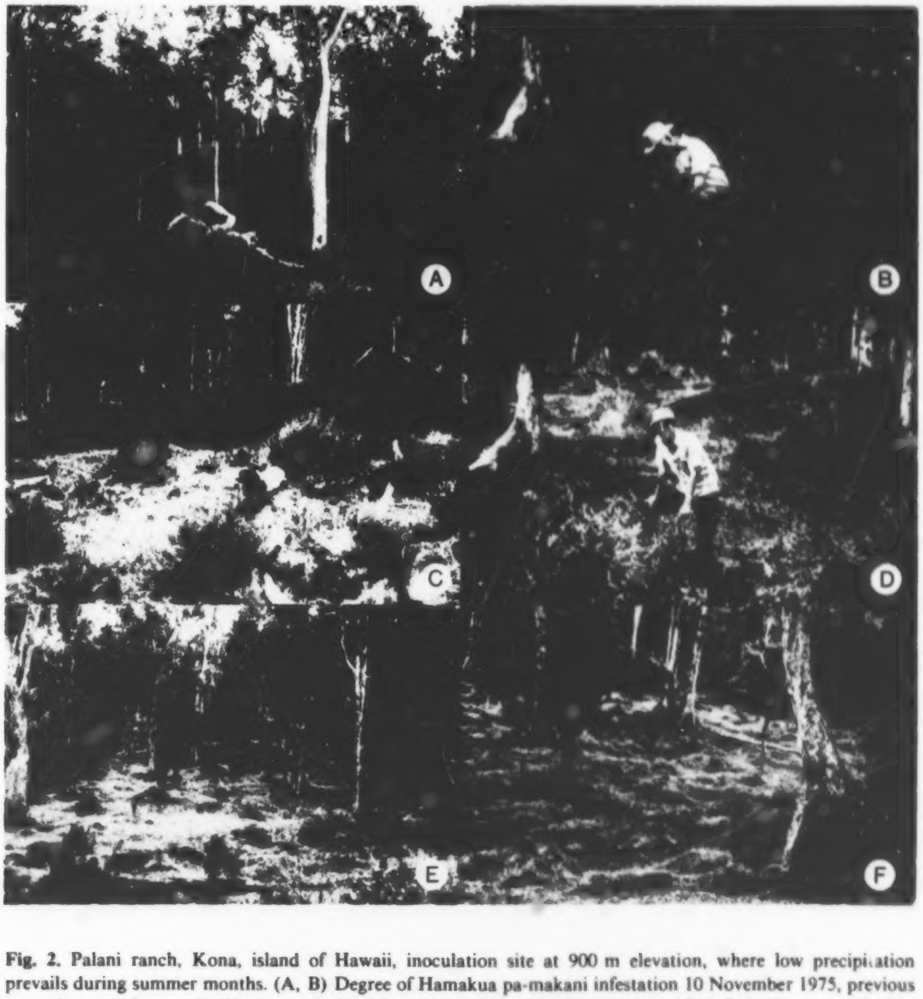

Fig. 2. Palani ranch, Kona, island of Hawaii, inoculation site at 900 m elevation, where low precipitation prevails during summer months. (A, B) Degree of Hamakua pa-makani infestation 10 November 1975, previous to pathogen release. (C) Weed population November 1976, showing recovery after first disease epidemics. (D) Degree of weed control, August 1979, 3 yrs after pathogen release. (E, F) 99% Hamakua pa-makani control January 1983, approximately 8 yrs after pathogen release.

On 10 November 1985, a water suspension of spores at 16°C was carried by plane to Hawaii and was used to inoculate by wetting the surface of 100 leaves at 4 sites in the upcountry range lands of Palani ranch, Kona. Approximately 500 ml of inoculum containing 200,000 spores/ml were used at 900, 1100, 1350, and 1500 m elevation. The areas selected for this study were 70–80% invaded by Hamakua pa-makani (Figs. 2-A, B; 3-A, D). Observations made 15 days later showed well developed lesions at inoculation sites 900 and 1100 m elevation, but none at 1350 and 1500 m. Lesions were visible at the higher elevations 30 days after inoculation and instead of chlorotic specks on the upper leaf surface the symptoms appeared as purple spots. The anthocyanin formation around the lesions was attributed to prevailing low temperatures (< 10°C at night).

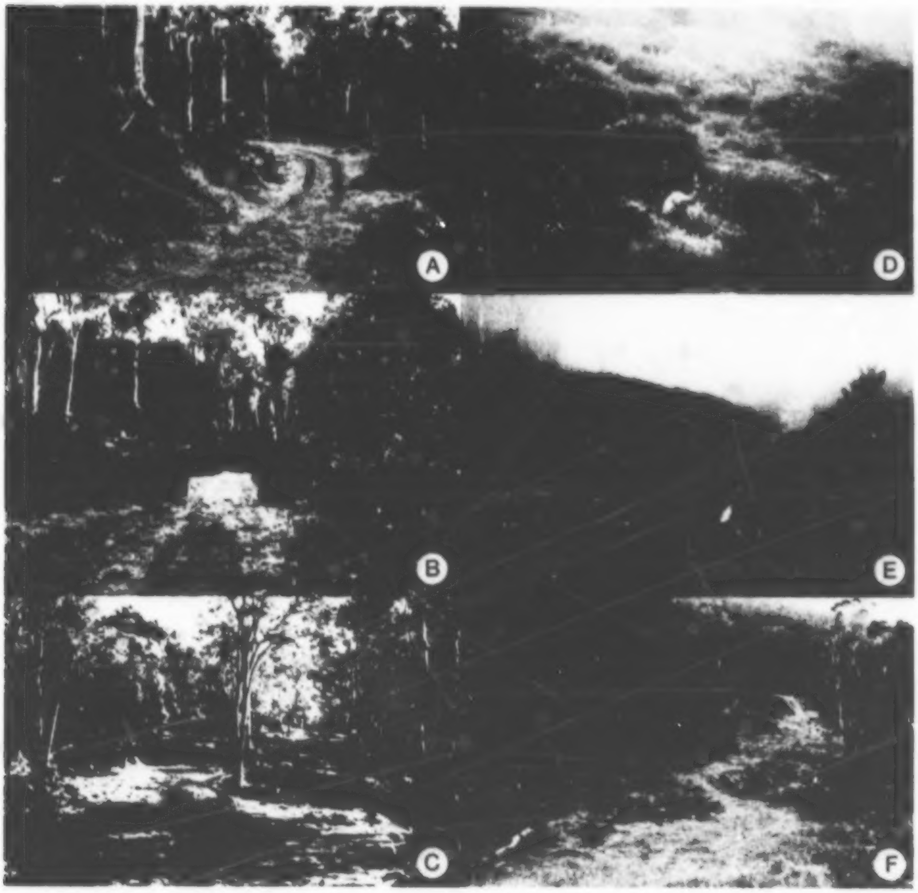

Fig. 3. Palani ranch, Kona, island of Hawaii, inoculation sites with high rainfall during the summer months, at 1000 m (A–C) and 1500 m (D–F) elevations. (A, D) Weed infestation previous to pathogen release 10 November 1975. (B, E) Massive disease epidemics May 1976, approximately 7 months after pathogen release. (C, F) Degree of Hamakua pa-makani control September 1978, approximately 3 yrs after pathogen release.

On 26 February 1976, a water suspension of > 200,000,000 spores was sprayed at random on *A. riparia* plant population within 500 ha of Palani ranch land, ranging in elevation from 600–1800 m. Weed population was estimated at 70–80% of the total biomass of the area. Monthly disease surveys showed 5, 20, 50 and 95% disease, respectively, 2, 3, 4 and 6 months after inoculation. The epidemic of the disease was so severe that the plants had very sparse foliage by the end of November and the following year blooming was noticeably reduced. The disease spread to adjacent non-inoculated weed areas by means of airborne spores which were blown in all directions by prevailing wind currents and deposited later by rain on the host. Four months after the initial inoculations in the island of Hawaii the pathogen was found on Hamakua pa-makani plants growing on Maui, in the vicinity of the Seven Sacred Pools, some 120 km from Kona, across the Hawaii-Maui Channel.

The disease initially developed more rapidly at the 900 and 1100 m sites than at 1350 and 1500 m; temperatures were more favorable at the lower elevations during the winter months. As summer temperatures began to climb, the disease incidence increased at the higher elevation and control of the plant became noticeable in the humid high country. The control of Hamakua pa-makani by *Cercosporella* sp. at Palani ranch has been extremely successful, and where there was 70–80% pa-makani there is now 70–80% Kikuyu grass pasture (Figs. 2–3).

Annual disease surveys done in Hawaii have shown > 95% control of the weed in less than a year after inoculation, on most areas with average annual rainfall of > 1.8 m and optimal temperatures for disease development during the wet periods. In areas with adequate moisture but lower than optimal temperatures for disease development, control > 95% was attained 3–4 yrs after inoculation. In areas with lower or higher than optimal temperatures for disease and low rainfall, the control has been < 80% after 8 yrs of pathogen release.

The successful biological control of *A. riparia* with *Cercosporella* sp. in Hawaii correlates with a number of favorable epidemiological factors influencing the rate of inoculum increase and distribution; e.g. high rainfall at the initial release sites; prevalence of temperatures favorable to the pathogen; and presence of a large infestation of Hamakua pa-makani. The rapid distribution of the pathogen soon after release was similar to the distribution of the skeleton weed rust in the Wagga Wagga area of Australia (Cullen *et al.* 1973). However, it was accomplished in less time and perhaps with fewer generations of the pathogen. The devastating ensuing epidemics in wet, optimal temperature sites of Oahu, Hawaii and Maui compared favorably with the late blight epidemics that destroyed Ireland's potato crops in 1945–46 (Large 1946). These results have led to the conclusion that host-specific fungal pathogens are safe and beneficial tools in exotic weed control. This is supported by the evidence that after 8 yrs of pathogen release the fungus still remains host-specific under many environmental conditions.

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The Role of Disease in Removal of Weed Species from Developing Forest Stands

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Abstract

Early colonizers of cut-over or burned forest land may dominate some sites for long periods and hinder the development of crop trees. Competition, insects and disease contribute to the decline of early colonizers with consequent release of crop trees, but the relative importance of these factors has not been determined. To evaluate the role of a disease, young thickets of pin cherry (*Prunus pensylvanica*) were studied in relation to the black knot disease caused by *Apiosporina morbosa*. Healthy pin cherry on large clear-cuts and burns were inoculated by placing cankered trees among them during bud break, and over the next five years, mortality and decline in height increment could be associated with infection. Establishment of the disease 2–4 yrs after a disturbance appears necessary for practical control. In small openings not affected by fire, natural infection may provide adequate control.

Rôle des Maladies dans la Lutte contre les Espèces de Plants Nuisibles Proliférant dans les Jeunes Peuplements Forestiers

Les colonisateurs précoces des terres déboisées ou des forêtes brûlées risquent de dominer certains sites pendant de longues périodes et, par conséquent, de nuire à la croissance des arbres pleriécolte. La concurrence, les insectes et les maladies permettent de diminuer le nombre de colonisateurs précoces, ce qui assure ultérieurement le développement des arbres periécolte; l'importance de ces facteurs est cependant difficile déterminer. On a tente de le faire dans le cas d'une maladie en étudiant les effets des nodules noirs causés par *Apiosporina morbosa*. sur de jeunes fourrés de petits merisiers (*Prunus pensylvanica*) Le taux de croissance de petits merisiers recouverts de chancres était légèrement inférieure à celui de spécimens sains similaires des zones adjacentes. En outre, les plants malades avient une espérance de vie plus courte dû à la compétition entre les arbres et à la défoliation par les insectes. L'inoculation des jeunes arbres sur de vastes zones entièrement coupées et brûlées a été effectuée par l'introduction de chancres en état de sporulation au moment de l'éclatement des bourgeons; durant 3 ` 5 ans suivant l'inoculation, le taux de mortalité et les faibles taux de croissance des cimes ont, dans une certaine mesure, pu être associés à une forte infestation. Pour des raisons pratiques, il semble nécessaire d'introduire la maladie dans les trois ou quatre ans qui suivent une perturbation pour assurer une lutte efficace. Dans les zones restreintes non incendiées, l'infestation naturelle semble fournir un contrôle adéquat.

Introduction

Biological control of unwanted species in the early stages of forest stand development presents different problems than those encountered in controlling weeds of agricultural crops or urban environments. First, the large areas involved in forest management require an approach that is economical and relatively simple. Second, the nature of the weeds themselves differ, being mainly native species which are present on the site in the form of buried seed or dormant buds at the time of removal of the old stand.

They are the pioneer species which colonize a site after a major disturbance such as fire or cutting and they usually have beneficial as well as detrimental roles. In some localities or in future economies they may have commercial value and many of them are closely related to commercial crops.

Current tactics in biological control have been placed in two categories, the classical and the bioherbicide (Templeton and TeBeest 1979). The classical tactic of introducing foreign organisms can be eliminated as a logical approach. The bioherbicide tactic, i.e. introduction of the pathogen earlier in the season or earlier in the life of the host than it would normally become established, might be feasible if economical and simple methods for massive inoculation are developed. A third approach, which I will call the silvicultural tactic, would involve manipulating stand conditions in such a way that diseases of weed species are favored. This will be considered at the end of the paper.

The species which are considered weeds vary with the forest region and the economy. Some of those in eastern Canada are as follows:

Kalmia angustifolia L. (Ericaceae), the sheep laurel or lambkill, on black spruce cutovers, barrens and blueberry fields (Damman 1971; Hall *et al.* 1973; Strang 1972);

Acer spicatum Lam. (Aceraceae), the mountain maple, on balsam fir and mixed-wood sites (Post 1969; Vincent 1965);

Pteridium aquilinum (L.) Kuhn (Dennstaedtiaceae), the bracken fern, on a variety of forest sites after a disturbance (Martin 1955; Place 1952);

Rubus strigosus Michx. (Rosaceae), the bramble or wild red raspberry, on cut-over spruce-fir sites (McCormack *et al.* 1978);

Prunus pensylvanica L. (Rosaceae), the pin cherry, on cut- or burned-over hardwood, mixed-wood or spruce-fir sites (Marks 1974);

Populus tremuloides Michx. (Salicaceae), the trembling aspen, on a variety of mesic sites;

Fagus grandifolia Ehrh. (Fagaceae), the American beech, on rich hardwood sites, forms thickets of slow-growing stems which are unmerchantable because of the beech bark disease.

Because all of the above species, as well as several that are not mentioned, are native to North America and are either related or sometimes are themselves commercially important, the classical tactic of introducing foreign organisms has not been considered. The bioherbicide tactic has had limited investigation, perhaps the most promising results to date being those of French and Schroeder (1969) on the control of oaks using the oak wilt fungus. Attempts to control sheep laurel, huckleberry (*Gaylusscia baccata* [Warg.] K. Koch; Ericaceae), and raspberry by mass inoculations with cultures of native pathogens showed little promise (Wall 1977, 1983).

The interactions among weed species on a developing forest site merit consideration in biological control. On the richer forest sites in the Maritime provinces a wide variety of species colonize a site after harvesting but these are often dominated by raspberry and/or pin cherry (Wall 1983). Early development of the latter tends to suppress the former, while either can dominate certain sites to the exclusion of most other vegetation. Of the two, early development and dominance by pin cherry is probably preferable since it does not produce the tangled mat of stems characteristic of raspberry.

Early dominance by one species to suppress other weed species requires that the chosen species be removed early enough to allow optimum development of crop trees, but not so rapidly that other weed species are released. Biological control should be preferable to herbicides in achieving this goal. Pin cherry has numerous diseases and insect pests and is normally short-lived in the presence of competing tree species. One very conspicuous disease that is usually abundantly present is the black knot canker caused by *Apiosporina morbosa* (Schw. ex Fr.) Arx. (Dothideales).

The black knot disease has a two-year cycle, beginning with infection of young shoots in spring, swelling of affected shoots the following spring and production of infective spores in the second spring (Koch 1934). Formation of a swelling or knot sometimes kills the portion of the stem or branch distal to the knot by impeding translocation. Infection of the main stem can cause dieback or death of the trees but the disease generally works slowly, not causing sudden mortality or growth loss. Growth analyses of adjacent healthy and diseased trees indicated a slight reduction in height increment and numbers of current twigs but no loss in diameter or volume growth (Wall 1981). To determine if the black knot disease plays a significant role in biological control, the disease was introduced into disease-free areas and its effects measured.

Methods and Materials

During the period of bud-break, heavily cankered pin cherry trees bearing sporulating stromata of the black knot fungus were cut and transported to burned- and cut-over areas where healthy, young pin cherry were abundant and where there were no nearby sources of natural infection. In each area, the cankered trees were spread out in a marked row. In subsequent years, 100 randomly selected codominant pin cherry trees at varying distances from the inoculated row were tagged and yearly records maintained of height, number of cankers, and mortality.

Results and Discussion

All of the areas in which diseased pin cherry trees had been placed were heavily infected by the black knot disease in the following year. In areas where natural infection was light or absent, i.e. large burned-over areas, the contrast between the general population and the trees in the immediate vicinity of disease introduction was immediately obvious. In all cases, a decline in numbers of cankers/tree was found as one moved from the row where diseased trees had been placed to a distance of 50–100 m from the row. The effect of wind direction at the time of spore dispersal was quite evident in some plots.

One large burned-over area in Nova Scotia was used for follow-up studies on the effect of disease introduction on subsequent growth and mortality. The trees were 3 yrs old and 0.5–1.5 m tall at the time of introduction. In the two study plots in this area, 15% of the inoculated trees died during the 5 yrs after introduction and another 30% developed top dieback, whereas only 2 and 10%, respectively, were so affected in the uninoculated surrounds. There were negative correlations ($r = -0.44$ to $r = -0.51$) between the number of cankers/tree and subsequent annual height increments of codominant trees.

By introducing the disease 3 yrs after disturbance, dominance by pin cherry was broken during the subsequent 5 yrs. One wonders how much more effective the treatment might have been if the disease had been introduced 2 or 1 yrs after disturbance. Two yrs should be optimum, because at that age branching would allow a much greater number of infection courts than would be available at 1 yr, and infections would still be sufficiently close to the main stem and the base of the tree to cause a high percent of mortality. Sporulating stromata would then be formed by the time the stand is 4 yrs of age and this would result in further infection.

The practicality of introducing diseased material to large areas at the optimum time of sporulation and infection may present problems under current forestry practice.

However, there are means of early introduction compatible with good management. Since fire destroys the disease, control of fire is an obvious means. Pin cherry on burned-over areas tends to dominate the site and reach a much larger size than on clearcuts. Since the presence of older, infected trees is necessary for early establishment of the disease, minimizing the size of clearcuts, strip-cutting, or building of roadways several years prior to the actual harvest can be important in providing reservoirs of inoculum. This tactic may not be sufficiently manipulative to fit into the bioherbicide category and might better be termed silvicultural.

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Biological Control of Milk Weed (*Euphorbia heterophylla*) with Pathogenic Fungi

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Abstract

The milk weed (*Euphorbia heterophylla*) is widely distributed in most of the crop land in Brazil and is more important in the southern soybean-producing states. In the State of Paraná alone, it is estimated that about $1.6 million worth of herbicide will be spent in 1984 to treat 70,000 ha of badly infested areas. The main damage to soybean production is caused by the green stems of the weed that clog harvesting machines and also transfer moisture to harvested beans. *E. heterophylla* has been found naturally infected by seven pathogenic agents (*Euphorbia* mosaic virus; *Uromyces euphorbiae*; *Sphaceloma* sp.; *Alternaria* sp.; *Helminthosporium* sp.; *Rhizoctonia solani*; and *Sclerotinia sclerotiorum*). Under experimental conditions, *Alternaria* sp. and *Helminthosporium* sp. were highly efficient and are promising as biological agents for the control of *E. heterophylla*. They have the advantage of being easily cultured under laboratory conditions.

Le Biocontrôle de la Mauvaise Herbe *Euphorbia heterophylla* L. au Moyen de Champignons Pathogéniques

La mauvaise herbe *Euphorbia heterophylla* est bien répartie dans la plupart des terres agricoles du Brésil, mais elle est plus importante dans les états du sud, ou se trouvent les plantations de soja. On estime que, dans le seul état de Paraná, on dépensera 1.6 million de dollars environ en 1984, en herbicides, pour traiter 70,000 ha des régions gravement infestées. Le dommage principal au rendement du soja resulte des tiges vertes de la mauvaise herbe, qui bouchent la moissoneuse et qui en même temps transfèrent de l'humidité à la récolte. On a observé sept agents pathogènes qui infectent *E.-heterophylla* de façon naturelle: le virus mosaique d'*Euphorbia*; *Uromyces euphorbiae*; *Sphaceloma* sp.; *Alternaria* sp.; *Helminthosporum* sp.; *Rhizoctonia solani*; et *Sclerotonia sclerotiorum*. Dans des conditions expérimentales, *Alternaria* sp. et *Helminthosporum* sp. se sont revelés hautement éfficaces et promettent bien pour le biocontrôle d'*E. heterophylla*. Ces agents ont l'avantage de se prêter facilement à la culture en laboratoire.

Introduction

Most weed plants of crop land in Brazil are controlled by chemical mechanical, or manual means, but a few remain that are more difficult to handle. One of the most difficult to control has been the milk weed, *Euphorbia heterophylla* L. (Euphorbiaceae).

The weed is widely distributed in most agricultural land in Brazil but is more important in the southern soybean-producing states.

Being resistant to most herbicides it has selectively survived chemical control and has become economically important in the past 5–6 yrs. If weather conditions are favorable, the weed produces seed and germinates all year round, frequently requiring more than one herbicide application during a crop season. Available herbicides are expensive, and more than one application could be economically unfeasible. Of several commercial herbicides currently used only one (Blazer) (sodium 5-[2-chloro-4-

(trifluoromethyl) phenoxy]-2-nitrobenzoate) (Rohm & Haas Co.) is effective against *E. heterophylla* (Gazziero *et al.* 1983).

For control of *E. heterophylla* alone, and only in the State of Paraná where about 70,000 ha of crop land will require chemical control, an estimated $1.6 million worth of herbicide will be spent in 1984.

In recent years, increasing awareness of undesirable effects of agricultural pesticides have resulted in stronger legislation regulating use and recommendation of chemicals for crop protection. As a consequence, more effort and funds have been directed toward biological control of crop pests.

Biological control of soybean and sugar-cane insects with pathogens are routinely used in Brazil but research on weed control is at the embryonic stage. The only reference on pathogens associated with *E. heterophylla* is in Viegas (1961).

Preliminary studies with biological agents have shown excellent results under experimental conditions.

Research carried out to date (Yorinori 1984) has dealt with: studies on the biology of *E. heterophylla*; surveys of pathogens associated with the weed; and evaluation of efficiency of the pathogens in control of *E. heterophylla* as compared with the herbicide Blazer.

Observations on the biology of *E. heterophylla* have shown that most infestation occurs from early December to February (Fig. 1) coinciding with early development to pod-filling stages of soybeans. The highest incidence of pathogenic agents has occurred from late December to end of February (Fig. 2).

In general, association of pathogens in the field does not prevent the weed for producing seed. They may cause severe defoliation, but leave the green stems. Stems cause clogging of harvesting machines and are most damaging to soybeans for conferring moisture to harvested beans.

Disease surveys on *E. heterophylla* have shown that the weed is naturally infected by at least seven pathogenic agents: *Euphorbia* mosaic virus; the rust, *Uromyces euphorbiae* (Ke. & Pk.) (Uredinales); the scab, *Sphaceloma* sp. (*Sphaceloma kruggii* Bitanc. & Jenkins?) (Coelomycetes); the leaf spot, *Helminthosporium* sp. (Hyphomycetes); the leaf spot and stem canker, *Alternaria* sp. (Hyphomycetes); a damping-off and root rot fungus, *Rhizoctonia solani* Kühn (Agonomycetes); and *Sclerotinia sclerotiorum* (Lib.) de Bary (Agonomycetes).

The first five pathogens were found consistently associated with *E. heterophylla*, and occur simultaneously when there was maximum infestation of the weed. *R. solani* and *S. sclerotiorum* occur in certain soybean producing regions but are also very destructive to soybean.

Under experimental conditions, only *Alternaria* sp. and *Helminthosporium* sp. have been shown to be highly efficient and promising as biological control agents. They have the advantage of being easily cultured in the laboratory. Under natural conditions these two fungi are generally found causing minor disease.

Greenhouse inoculations with isolates of *Alternaria* sp. and *Helminthosporium* sp., showed that both fungi caused significant reduction of fresh weight of *E. heterophylla* 72 h after inoculation (Table 1). *Helminthosporium* sp. was as efficient as the herbicide Blazer.

Helminthosporium sp. was extremely virulent in greenhouse tests. It was capable of colonizing leaf tissue in less than 6 h of incubation time (Fig. 3); with 12 h or more it caused complete defoliation within 72 h when inoculated on 32-day-old plants with inoculum containing 1×10^4 spores/ml. The first lesions were visible within 12–14 h after inoculation.

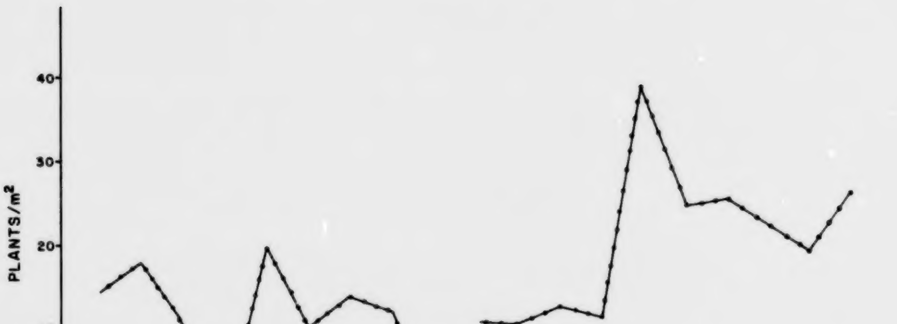

Fig. 1. Fluctuation of *Euphorbia heterophylla* L. population (plants/m^2) in the field. Period of observation: 27 November 1981 to 19 February 1983.

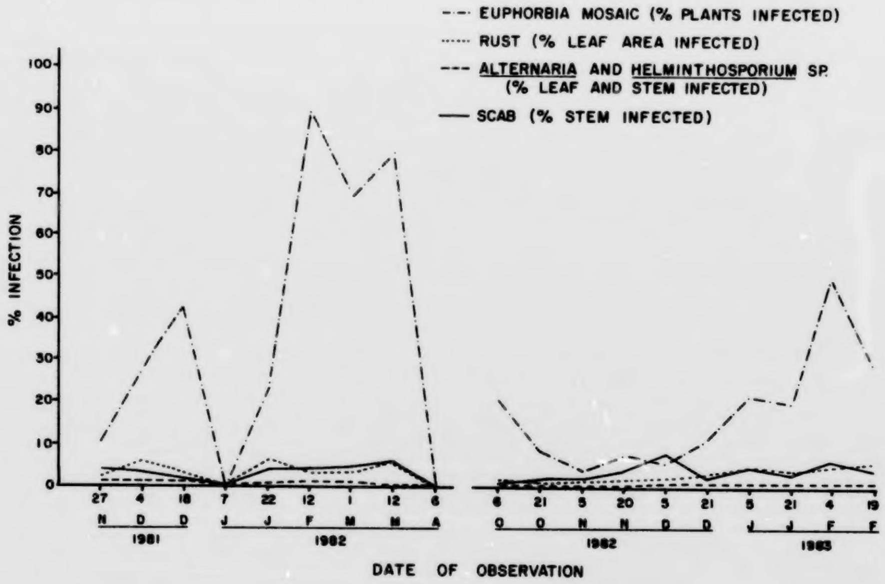

Fig. 2. Disease incidence on *Euphorbia heterophylla* L. under field conditions. Period of observation: 27 November 1981 to 19 February 1983.

Table 1. Effect of pathogenetic fungi and herbicide Blazer on control of *Euphorbia heterophylla* L. in a greenhouse experiment conducted in 1982.

Treatment[1]	Fresh weight[2] (g)	% reduction from control
Control (Water)	27.5 *a*[3]	0
EMG-1 (*Alternaria* sp.)	24.6 *ab*	10.5
EMG-2 (*Alternaria* sp.)	23.1 *ab*	16.0
EPR-2 (*Alternaria* sp.)	18.8 *bc*	31.6
C95-A (*Helminthosporium* sp.)	17.7 *bc*	35.6
Blazer (0.75 *l* /ha)[4]	14.4 *cd*	47.6
C95-A (*Helminthosporium* sp.)	8.7 *d*	68.4

[1] Treatment at 32 days after planting.

[2] Avg. of 5 replicates, 72 h after treatment.

[3] Numbers followed by the same letter are not significantly different ($P<0.05$).

[4] Blazer: Sodium 5-[2-chloro-4-(trifluoromethyl) phenoxy]-2-nitrobenzoate.

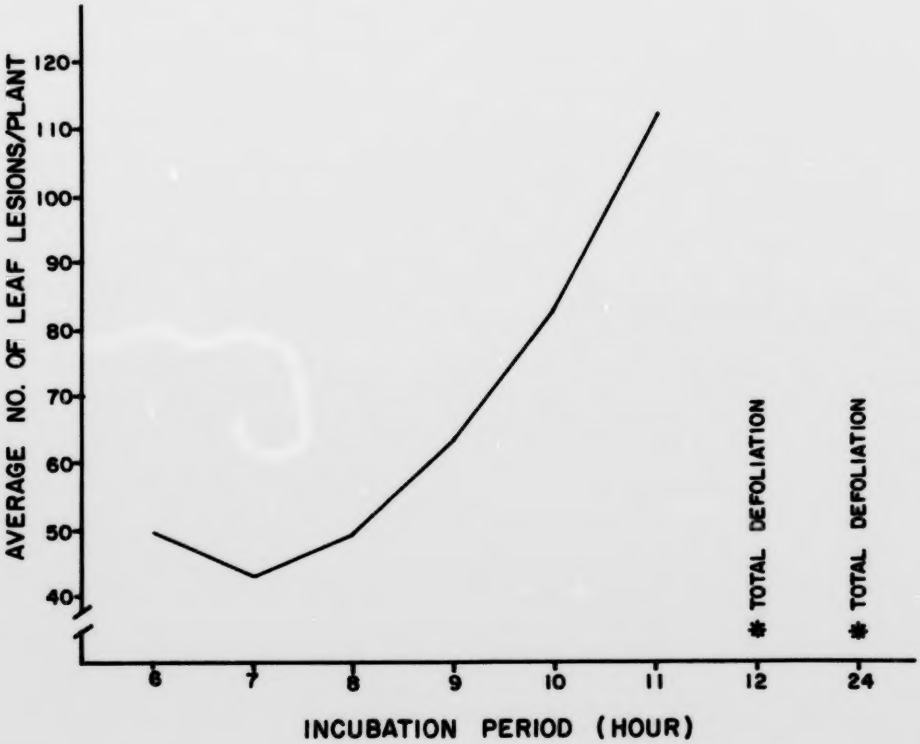

Fig. 3. No. of leaf lesions on 32-day-old *Euphorbia heterophylla* L. (plants 72 h after inoculation with *Helminthosporium* sp. and 6–24 h of incubation period. Experiment conducted in 1983.

Under field experiments, *Alternaria* sp. was less efficient requiring longer time to cause infection, but *Helminthosporium* sp. was as efficient as Blazer (Table 2). Inoculations were made when plants were flowering, thus under a condition when Blazer would not be recommended. Both *Helminthosporium* sp. and Blazer caused severe defoliation, preventing treated plants from producing seeds.

Almost all plants in the field experiment became infected by Euphorbia mosaic virus, but apparently seed production was not affected by the virus. *E. heterophylla* plants seem to be adapted to infection by the virus.

Alternaria sp. is less effective than *Helminthosporium* sp. in causing defoliation, but is effective in killing the plant by stem infection. A single stem infection at seedling stage can kill the plant. On the other hand, *Helminthosporium* sp. is efficient in causing defoliation, but causes only minor stem spots. A mixed inoculation with both *Alternaria* sp. and *Helminthosporium* sp. may result in greater control. This has not been tested.

An attempt to test the *Helminthosporium* sp. as a biological control agent of *E. heterophylla* in *c.* 2 ha of heavily infested soybeans did not reproduce the experimental results. The reason for this failure remains unknown.

Table 2. Effect of pathogenic fungi and herbicide Blazer on control of *Euphorbia heterophylla* L. in the field during 1982.

Treatment[1]	Dry weight[2] kg/8 m^2	% variation from control
EMG-2 (*Alternaria* sp.)	6.6 *a*[3]	11.86
C95-A (*Helminthosporium* sp.)	6.2 *a*	5.10
EPR-12 (*Alternaria* sp.)	6.0 *a*	1.69
Control (Water)	5.9 *ab*	0
EMG-1 (*Alternaria* sp.)	5.9 *ab*	0
Blazer (0.75 *l*/ha)[4]	5.0 *bc*	-15.25
C95-B (*Helminthosporium* sp.)	4.3 *c*	-27.12

[1] Treatment at early flowering stage.

[2] Avg. of 4 replicates; harvested 72 h after application.

[3] Numbers followed by the same letters are not significantly different ($P<0.05$).

[4] Blazer: Sodium 5-[2-chloro-4-(trifluoromethyl) phenoxy]-2-nitrobenzoate.

Current research is being conducted on: selection of more virulent isolates of *Alternaria* sp. and *Helminthosporium* sp.; development of culture media for mass production of spores; and evaluation of effects of environmental conditions on field infection by both fungi.

In addition to the naturally occurring pathogens, an application of *Alternaria* sp. and *Helminthosporium* sp. inocula at the early stage of weed development is expected to keep the weed population at a manageable level. Neither fungus has been shown to be pathogenic to crop plants.

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Chapter Eight
Reports

Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984,
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Transfer of Cinnabar Moth, *Tyria jacobaeae*, in Eastern Canada for Control of Tansy Ragwort, *Senecio jacobaea*

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Abstract

Attempts to establish the cinnabar moth, *Tyria jacobaeae* (Lepidoptera: Arctiidae), on tansy ragwort, *Senecio jacobaea* (Compositae), in Ontario by transfer of fourth- and fifth-instar larvae from established populations in Nova Scotia in 1979 and 1981 were not successful. Larval populations declined very rapidly with no apparent overwintering. In mid-June 1983, 470 cinnabar moth adults were netted in Nova Scotia and tansy ragwort leaves with 224 egg masses containing about 11,000 eggs were collected and flown to Ontario. Ten moths in flying condition and 147 weak ones were released immediately. About one day prior to egg hatch, leaves with egg masses were paper-clipped to healthy leaves on tansy ragwort plants at two release sites. Larvae from about 10% of 10,000 released eggs passed the fifth instar under field conditions in 1983. In June 1984, several flying adults were observed at one site, followed by a population of about 450 larvae indicating survival of the insect through one complete generation under field conditions in Ontario. From 3000 late-instar larvae collected in Nova Scotia on 14 July 1983 and reared in laboratory cages at Guelph, 900 pupae were recovered. In June 1984, adults emerged from 15% of pupae held in peat moss at 2°C, 10% of pupae in peat moss in 75% r.h. over saturated salt solution at 2°C, and 12% of pupae in peat moss in plastic containers outside.

Introduction du Lépidoptère Tyria dans l'est du Canada pour la Lutte Contre le Séneçon jacobée

Les tentatives d'éstablissement de la tyria *Tyria jacobaeae* (Lepidoptera: Arctiidae) sur *Senecio jacobaea* (Composées) en Ontario par le transfert en 1979 et 1981 de larves des quatrième et cinquième stades de populations permanantes en Nouvelle-Écosse n'ont pas réussi. Les populations de larves ont diminué très rapidement, ne survivant pas à l'hiver. À la mi-juin 1983, 470 lépidoptères tyria adultes ont été capturés au filet et des feuilles de seneçon jacobée sur lesquelles avaient été déposées 224 masses d'oeufs englobant environ 11 000 oeufs ont été recueillies en Nouvelle-Écosse et transportées par avion en Ontario. À leur arrivée, seuls dix lépidoptères étaient en état de voler. Ces dix spécimens ainsi que 147 lépidoptères affaiblis ont été relâchés sur un site le 20 juin. Environ un jour avant l'éclosion des oeufs, les feuilles sur lesquelles reposaient les masses d'oeufs ont été attachées au moyen de trombones à des feuilles saines de plants de séneçon jacobée en deux emplacements. Les larves d'environ 10% des 10 000 oeufs introduits ont survécu au-delà du cinquième stade larvaire et ont atteint l'état de pupe dans les conditions du terrain. Des larves obtenues en laboratoire aux stades 1 à 3 et 2 à 4 ont été libérées sur deux autres sites. Le 14 juillet, 3 000 larves parvenues aux dernières étapes larvaires ont été recueillies en Nouvelle-Écosse pour terminer leur développement dans un laboratoire de Guelph. Environ 900 spécimens ont atteint le stade de pupe et sont actuellement soumis à l'état d'hibernation dans quatre séries de conditions différentes en vue d'être libérées au printemps de 1984.

Introduction

Tansy ragwort, *Senecio jacobaea* L. (Compositae) is a short-lived herbaceous perennial or biennial which has been introduced from Europe into North and South America, New Zealand, Australia, and South Africa. In Canada, this weed dates from about

1850 in the eastern Maritime provinces, being especially widespread in Prince Edward Island, eastern Nova Scotia and parts of New Brunswick where it is continuing to spread (Harris *et al.* 1971). Extensive infestations dating from about 1913 occur along the east coast of Vancouver Island and near Abbotsford in the lower Frazer Valley of British Columbia. In contrast to the extensive Maritime infestations on Canada's east and west coasts, a small, mid-continent infestation has persisted near Guelph, Ontario, since prior to 1927.

Although tansy ragwort does best in open, well-drained sites on medium soils, it will tolerate and persist under shade and in poorly-drained areas. It does not survive regular cultivation but establishes readily in newly-seeded pastures, in moderate to poor grass swards, and in undisturbed open areas where it may eventually form solid stands. In addition to reducing forage yield by competition with hay and pasture species, tansy ragwort contains toxic alkaloids which make it a hazard to livestock whether eaten fresh, in hay or in silage. Harris *et al.* (1971), in presenting a concise discussion of the pest status and biological control work against this weed in Canada, cited references which estimated that losses due to poisonings during 1968 were 30–50 head of cattle in King's County and 10–15 head in Queen's County, Prince Edward Island.

Attempts at biological control of tansy ragwort in Canada have centred on the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Acrtiidae), utilizing open releases of larvae and some adults imported from Sweden, Switzerland and California in the 1960s in British Columbia, Nova Scotia and Prince Edward Island (Harris *et al.* 1971). Establishment of the moth followed a pattern of high mortality of laboratory-reared stock during the first year after release, approximate maintenance of the larval population in the following two years and a four- to five-fold annual increase in the fourth and later years. Complete defoliation of the weed over 0.2 to 0.4 ha patches was observed by the third and fourth years. The cinnabar moth has continued to increase and spread and has been providing effective control in a variety of habitats on both eastern and western coasts of Canada (Harris, pers. comm.; Thomson, pers. comm.; Alex, unpubl. data).

The ragwort seed-fly, *Hylemya seneciella* Meade (Diptera: Muscidae), and the ragwort flea beetle, *Longitarsus jacobaeae* Wat. (Coleoptera: Chrysomelidae), have also been released and may provide supplemental pressure against the weed in areas where the cinnabar moth is established, as well as the only pressure in habitats where ecological restrictions on the moth prevent it from attacking the weed (Harris *et al.* 1971; Harris, pers. comm.).

Status of Tansy Ragwort in Ontario

The small infestation of tansy ragwort near Guelph, Ontario, was virtually ignored by weed control personnel for more than 50 yrs. The earliest record is a herbarium specimen deposited in the University of Guelph herbarium, collected in 'Oct. 1927' by I.E. Thomas and giving as locality: 'Oil Well Swamp near Puslinch Lake' [about 8 km southwest of Guelph]; habitat: 'Pastures, roadsides, waste places'; and remarks: 'Not common in this section'. Subsequent collections in 1934, 1951, 1952, and 1955 also specify the same locality. Their habitat data imply that the weed was persisting but not spreading. However, in 1974 and 1976 reports were received of the weed a few km distant. In 1977 it was observed established in about 10 sites scattered through a 10 km radius from the original 'Oil well swamp' site. A detailed survey in 1978 determined that it occurred in at least 52 parcels of land, with individual infestations ranging from a single plant in a well-maintained residential lawn to numerous small and large dense patches throughout a 20 ha permanent pasture on rolling gravelly soil (Alex, unpubl. data). The majority were located within 10 km of the original infestation but the range extended in an ellipse about 40 × 20 km. The weed occupied such a wide variety of habitats that effective control or containment by herbicides or cultivation was judged impractical.

Evidence indicates that tansy ragwort failed to survive at two other sites in Ontario. Herbarium specimens deposited with Agriculture Canada, Ottawa (W.J. Cody, pers. comm.) and the University of Guelph give one locality as Niagara Falls in 1903 and the other as Ottawa in 1932 but the weed has not been reported from either locality since those original collections were made.

Because tansy ragwort was apparently spreading rapidly in the Guelph area, because it was circumstantially implicated in cases of livestock illness, and because Harris *et al.* (1971) recommended the cinnabar moth as a promising biological control agent against this weed, a program was initiated in 1979 to introduce and establish the insect at Guelph.

Methods and Materials

Three attempts were made to transfer the cinnabar moth from Nova Scotia to Guelph. On 13 July 1979, 5500 larvae, mostly in fourth- and fifth-instar, were collected near Durham and Toney River, Nova Scotia, packaged in lots of 500–1000 with fresh tansy ragwort foliage in plastic bags, placed with block ice in styrofoam picnic coolers, and shipped by air as checked baggage to Ontario. The next day the surviving larvae were counted, provided with fresh foliage and released as follows: open release of 1013 on dense patches of the weed in the fenceline of a grazed pasture on well-drained, level loam soil on 14 July; open release of 1018 in an old alfalfa, *Medicago sativa* L. (Leguminosae), field on undulating, well-drained loam soil on 14 July; open release of 846 and cage release of 200 in a fenced-off portion of a grazed pasture on rolling, gravelly loam on 16 July; and open release of 1002 and cage release of 400 in a lightly-grazed pasture on moderately-drained, stony clay loam soil on 16 July. The release sites were monitored at two-day intervals.

The second attempt was 24 July 1981. About 2000 fourth- and fifth-instar larvae were collected in the morning in Nova Scotia, packaged as before but in smaller lots, flown to Ontario in the afternoon and open-released that evening at two locations near Guelph. One was an ungrazed pasture (Site 52) on a gentle south slope on sandy loam soil. The other (Morriston) was in a heavily-grazed pasture on rolling gravelly loam soil. These releases were monitored at one- to two-day intervals.

Between 16 and 19 June 1983, 470 adult cinnabar moths were netted near Antigonish, Nova Scotia, and leaves with 224 egg masses containing about 11,000 eggs were collected in the same area. These were packaged with ice in insulated boxes and flown to Ontario. On 20 June, 10 vigorous flying adults and 147 weak adults were released at Site 52. About one day prior to egg hatch (when egg colour changes from yellow to grey), leaves bearing egg masses were paper-clipped to healthy leaves on vigorous plants at each release site. In this way, about 5000 eggs were released 21 and 22 June at Site 52, and about 5000 from 23 to 25 June at the Morriston site. Of the 1000 eggs which emerged in the laboratory, 500 first- to third-instar larvae were released 24 June on a moderately-dense stand of the weed on poorly-drained organic soil (Cedar Swamp site) and another 500 second- to fourth-instar larvae on 27 June on a stand of the weed around the edge of a small pond in strongly rolling stony loam soil (Crawley's Pond site).

Attempts to make detailed counts of the young larvae at Site 52 in early July had to be abandoned because many dropped off the plants with such slight disturbance as touching or walking past. However, general monitoring was continued until there was no further sign of any larvae.

On 15 July 1983, 3000 late-instar larvae were collected in Nova Scotia, packaged as before, flown to Ontario and placed in rearing cages in the laboratory the same evening. These larvae were regularly supplied with fresh tansy ragwort foliage and allowed to pupate in mineral soil or peat moss. Of the 900 pupae so obtained, 200 were overwintered in peat moss at 2°C, 200 in peat moss over a saturated salt solution to maintain 75% r.h. at 2°C, 300 unprotected over a saturated salt solution at 2°C, and 200 in peat moss in plastic containers with metal screen vents in an outside storage area. All but 300 of the pupae were removed from storage in June 1984 and placed in cages to emerge. Emerged adults were then released at the Morriston and Crawley's Pond sites. The remaining 300 were removed in late July, allowed to emerge in cages and lay eggs on fresh foliage and then the adults, with 150 of their own larvae, were released at the Morriston site on 29 July.

All release sites were examined at intervals during each succeeding year, searching for evidence of successful overwintering and subsequent egg-laying.

Results and Discussion

The 1979 shipment of larvae resulted in about 20% mortality on arrival in Guelph. Most of this appeared due to drowning in a pool of water which had accumulated at the bottom of each plastic bag; the moisture coming from the fresh foliage added to the bags just before packaging and from respiration of the insects, which condensed on the inner surface of the plastic bags adjacent to the ice blocks. Mortality was virtually nil in the 1981 and 1983 shipments of larvae because the number of larvae in each individual plastic bag or firm plastic container was reduced to only 100–500, and the time lapse between collecting and releasing was reduced to < 12 h.

In both 1979 and 1981, numbers of larvae observable at release sites declined very rapidly after release. Within two days, the numbers had dropped to < 30%. After four days only about 5% of the larvae were seen, and all had disappeared by seven days after being released. We assumed the decrease was due to predation, although there had been little observed predation of the larvae on the plants by birds, mammals or other insects during daylight hours. Because we observed little predation at any site, it was therefore assumed that most larvae had passed their fifth instar and were pupating. However, limited digging through the surface soils of these release sites after the larvae had disappeared failed to turn up any pupae. Wilkinson (1965) reported that high mortality in British Columbia resulted when, as the larvae descended to the ground to pupate, they were attacked by carabid beetles. The same may have happened here because carabids were also present at all release sites.

Both the 1979 and 1981 releases of larvae were judged to have failed when, in subsequent years, there were no observed flights of adults, no egg laying, and no new populations of larvae. This was not surprising in that Harris *et al.* (1971) reported that 12 of 15 open releases of larvae from 1962–67 in both eastern and western Canada had failed to establish.

The 1983 releases of eggs, however, resulted in substantial populations of larvae in 1983 followed by survival into 1984. Detailed counts were not made in 1983 because young larvae fell off plants very readily, but it was estimated that larvae from 10% of the released eggs at each site passed the fifth instar and descended from the plants to pupate. This would have represented about 500 from released eggs at each of Site 52 and the Morriston site, and 50 from young laboratory-hatched larvae released at the Cedar Swamp and Crawley's Pond sites. The only predation observed in 1983 was an unidentified species of stink bug (Pentatomidae) sucking on one early fourth-instar larva.

The first indication of overwinter survival of the cinnabar moth in Ontario was the appearance of three adults flying on 15 June 1983, at Site 52. This was followed by 12 adults flying on 18 June and three on 20 June. Six egg masses, totalling over 300 eggs were found. All were presumed fertile, after one mass with 69 eggs hatched completely after being removed to the laboratory. By 25 June clusters of second-instar larvae were seen feeding near two of the egg masses. During the next 4 wks the numbers of larvae increased to an estimated 450 and they became well dispersed throughout the 0.2 ha release site. A detailed count on 24 July recorded 165 fourth- and fifth-instar larvae. This count was taken after the population had decreased by about two-thirds from those observed the previous week as the fifth-instar larvae had begun to leave the plants. At Site 52 the sequence of an estimated 500 larvae passing fifth instar in 1983, followed by about 450 larvae in 1984 approximates the first 2 yrs of the establishment pattern described by Harris *et al.* (1971), in which there was high mortality during the first year followed by approximate maintenance of larval populations in the following 2 yrs.

At the Morriston site one flying adult was observed on 20 June 1984. However, as that was the only adult seen and as neither egg masses nor colonies of larvae could be found later, the population did not successfully overwinter at this site.

There was no apparent overwintering survival at either the Cedar Swamp site or at the Crawley's Pond site which had been seeded with laboratory-emerged larvae in 1983.

Overwintering pupae in peat moss held at 2°C in a plastic container resulted in 15% emergence of adults in 1984, whereas 12% survived storage in peat moss in the outdoor compound, 10% in peat moss in 75% r.h. over a saturated salt solution at 2°C, and nil when unprotected over the same saturated salt solution.

All adults from the first group of artificially overwintered pupae were released at the Crawley's Pond site as they emerged. They produced several groups of larvae which fed extensively on the weed. On 20 July, there were about 70 fifth-instar larvae, but by 25 July this number had dropped to 32.

The collection of cinnabar moth larvae in Nova Scotia and their release on field stands of tansy ragwort in Ontario has failed to establish the insect here. On the other hand, collecting tansy ragwort leaves bearing egg masses, holding them until just prior to hatching, and clipping them to healthy leaves of established plants at the release site has resulted in survival of the insect through one complete generation. This parallels the experience of Harris *et al.* (1971) in those releases which resulted in successful establishment of the cinnabar moth.

Acknowledgments

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A Survey to Evaluate the Long-term Relationship Between *Chrysolina quadrigemina* and its Host-weed, St. John's Wort, in Southeastern Australia

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Abstract

The design and setting up of a long-term survey to evaluate the overall impact of *Chrysolina quadrigemina* on St. John's wort is described. Information is being gathered by questionnaire three times/yr from 108 sites throughout the range of the weed in southeastern Australia. This data covers: (1) details of the St. John's wort infestation; (2) the size of *C. quadrigemina* populations and damage caused by them; and (3) management practices used at the site. Data of climatic and physical variables are also being obtained. Some early results are shown. Preliminary analyses of these indicate that the survey will be able to quantify geographic and temporal trends in the interaction between *C. quadrigemina* and St. John's wort. In addition, they show that it should be possible to identify factors which modify this interaction.

Évaluation des Relations à Long Terme Entre *Chrysolina quadrigemina* et la Plant Nuisible Hôte, le Millepertuis Perforé, dans le Sud-est de l'Australie

Le rapport traite de la conception et de l'organisation d'une étude à long terme destinée à évaluer les effets globaux de *Chrysolina quadrigemina* sur le millepertuis perforé. Des questionnaires sont distributés trois fois l'an dans 108 sites de l'aire de répartition de cette plant nuisible dans le sud-est de l'Australie. Les questionnaires portent sur: (1) le degré d'infestation du millepertuis perforé; (2) la taille des populations de *C. quadrigemina* et leurs effets sur la plant nuisible; et (3) les techniques de gestion employées sur le site. On rassemble aussi les données sur les paramètres climatiques et physiques. Le rapport présente certains résultats préliminaires. Les premiéres analyses ont révélé qu'il sera possible de quantifier les tendances spatiales et temporelles de l'interaction entre l'agent biologique et la plant nuisible. En outre, d'après cette analyse, il devrait être possible la reconnaitre les facteurs qui modifient cette interaction.

Introduction

The aim of introducing biological control agents is to bring about a reduction in the population of the target weed to a lower equilibrium density, below that of its economic threshold (van den Bosch *et al.* 1973) (Fig. 1*a*). Unfortunately, as Harris (1981*a*) has pointed out, many agents, although they may establish, do not have this effect. Species may stabilize at low population levels which have little impact on weed density (Fig. 1*b*), or their population density may fluctuate widely, resulting in reductions of the target weed which may not be maintained (Fig. 1*c*). Agents which show such partial success are, however, an important component of control procedures against particular weeds, for they contribute to the stress load on the plant (Harris 1981*b*). Therefore, it is desirable to assess the impact of such an agent to understand how it might interact with additional stress factors (e.g. grazing pressure, plant competition, drought, the introduction of additional biological control agents and the use of herbicides) which might lead to more effective control of the weed.

Given time, such agents are likely to have colonized a range of habitats containing the weed, and their impact may vary markedly between localities as well as with time.

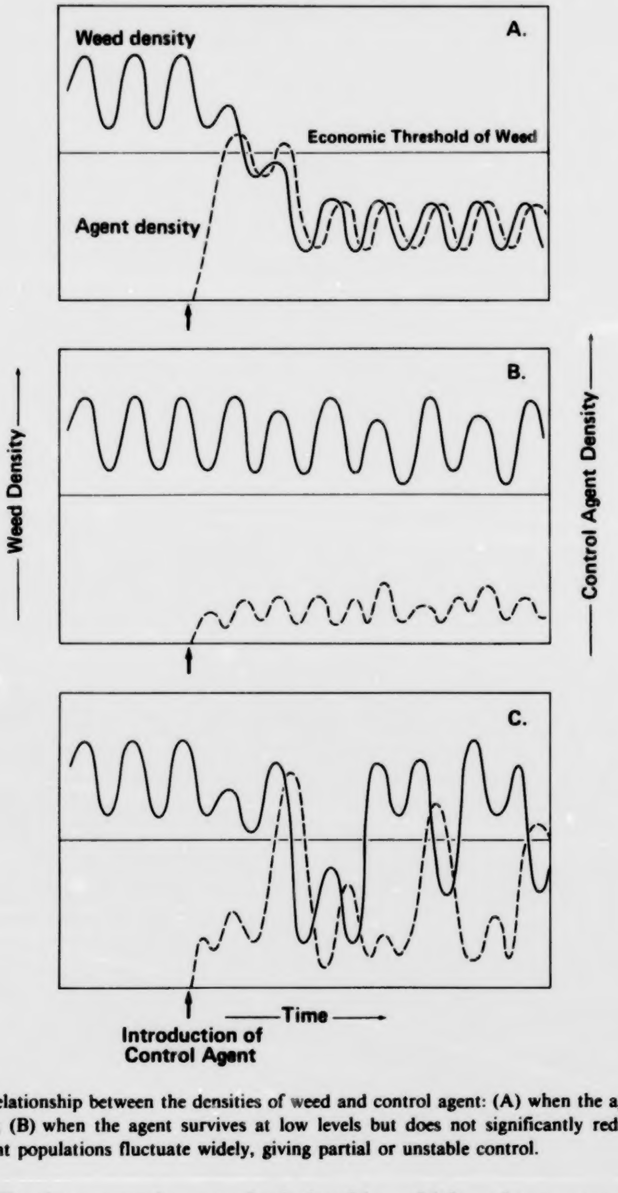

Fig. 1. Expected relationship between the densities of weed and control agent: (A) when the agent successfully controls the weed; (B) when the agent survives at low levels but does not significantly reduce weed levels; and (C) when agent populations fluctuate widely, giving partial or unstable control.

Thus, there will exist a complex set of relationships which make an overall evaluation of the agent a difficult task. Such a study would require the collection of data over a wide area and over a long period of time, an exercise which could have serious logistic and financial constraints. One possible solution would be to organize a survey network where data can be collected by individuals at diverse localities and collated at a central point. If the collection of the data were kept simple it could be carried out routinely over an extended period with minimal cost in time or money.

This paper outlines the design of such a long-term survey to evaluate the overall impact of *Chrysolina quadrigemina* Suffr. (Coleoptera: Chrysomelidae), a defoliating beetle which has shown partial success against St. John's wort (*Hypericum perforatum* L.; Clusiaceae) in southeastern Australia.

The *Chrysolina*–St. John's Wort System in Southeastern Australia

C. quadrigemina was first released in northeastern Victoria in 1939. Larvae and adults defoliate St. John's wort, in winter and spring respectively, and initially the species showed great promise and contributed to the successful control of the weed in certain areas near the original release site (Wilson 1960). This led to a massive redistribution program which continued intermittently until the mid-1960s. As a result, *C. quadrigemina* is presently found through most of the range of its host weed (Fig. 2), and has coexisted with its host plant in most locations for 20–45 yrs. It does not yet occur in some areas to which St. John's wort has recently spread, such as western Victoria (Shepherd 1983).

Detailed evaluation studies undertaken a few years after establishment (Clark and Clark 1952; L.R. Clark 1953; N. Clark 1953) clearly demonstrated the limitations of *C. quadrigemina* in exercising effective control, by itself, over St. John's wort: its inability to colonize timbered areas, its slow rate of increase, and most importantly, the ability of St. John's wort infestations to regenerate following defoliation in the absence of other stress. This latter point was further emphasized by Huffaker (1966), who found that substantial summer rainfall, typical of many of the St. John's wort-infested areas of Australia, could promote regeneration following defoliation as well as upsetting the synchrony of reproduction and development in the beetles (*C. quadrigemina* adults undergo obligate aestivation over summer, which is broken by autumn rains prior to oviposition). Notwithstanding the above, Huffaker (1966) felt that *C. quadrigemina* provided sufficient additional stress on St. John's wort to make it an important factor in the control of the weed. He cited areas in northeastern Victoria where reclamation of large tracts of St. John's wort-infested land was attributed to the beetle. Since Huffaker's study, further reports of large infestations of St. John's wort being controlled by *C. quadrigemina* have been made for areas with predominantly summer rainfall, notably Mudgee, N.S.W., in the late 1960s (W. Ryan, pers. comm., 1982) and the Liverpool Ranges, N.S.W., between 1978–82 (I.R. Arnott and A. McMaster, pers. comm., 1982).

More typically though, *C. quadrigemina* behaves either as in Fig. 1*b*, in that populations of the beetle never reach levels which inflict significant reductions of infestation size, or as in Fig. 1*c*, in that populations periodically increase to damaging levels, but do not normally affect a lasting reduction in weed density. Because of this the beetle has generally been perceived as a failure in areas of high summer rainfall and in forested country. This led to a revival of the biological control program against St. John's wort by CSIRO Division of Entomology in 1979 (Delfosse and Cullen 1981).

This program involves the introduction of new control agents, such as the geometrid defoliator, *Anaitis efformata* Guenée (Lepidoptera: Geometridae), which is currently being released (Briese, unpubl. data). An established species such as *C. quadrigemina*, which is capable of periodically causing extensive defoliation, will have an important bearing on the success or failure of subsequent agents. For example, in the 1940s a colony of the root-borer, *Agrilus hyperici* (Creutzer) (Coleoptera: Buprestidae), was developing well in northeastern Victoria until the release area was repeatedly defoliated by waves of *C. quadrigemina* adults (T.G. Campbell, unpubl. data), and recent studies have shown that the autumn generation of *A. efformata* can be detrimentally affected when *C. quadrigemina* larvae defoliate St. John's wort (Briese, unpubl. data). Thus it is important to obtain information on the frequency and extent of such events, the factors that might contribute to their occurrence, and whether they are predictable.

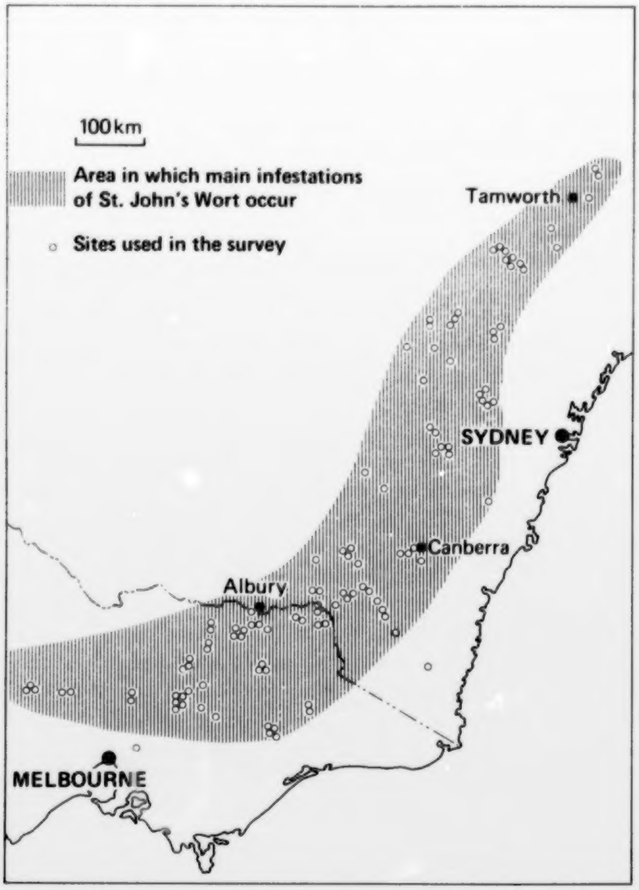

Fig. 2. Distribution of sites being used in the survey of the relationship between *Chrysolina quadrigemina* Suffr. and St. John's wort, *Hypericum perforatum* L., in southeastern Australia.

Moreover, in this program *C. quadrigemina* is being viewed as a contributory stress factor, as suggested by Huffaker (1966), rather than as a solution in itself. Thus it becomes important to understand the overall impact of the beetle. While earlier evaluation studies provided some answers, they were restricted to relatively short periods or to a few specific locations. It is hoped that by obtaining information on long-term changes and regional differences in both *C. quadrigemina* and St. John's wort populations, we might better understand what contributory stress factors are involved when the beetle is 'successful' and how the effect of the beetle might be best complemented. The success of a previous questionnaire survey in delineating the area of distribution of *Chrysolina* spp. and St. John's wort in Victoria (Shepherd 1983) offers promise that this more ambitious project will produce useful results.

Design of the Survey

The survey network consists of 108 sites throughout the range of St. John's wort infestations in mainland southeastern Australia (Fig. 2). One of the more important requirements of such a survey was to enlist observers with sufficient experience to ensure reliability of the data collected. This was provided by the help of State government Land Inspectors in Victoria and local government Noxious Weeds Inspectors in New South Wales. In addition, some private landholders, who had been particularly troubled by St. John's wort and who were interested in the biological control program, are taking part in the survey. In all, the 108 sites are being monitored by 39 observers (Table 1; see also Appendix 1).

Table 1. Summary of observers participating in the survey on long-term relationships between *Chrysolina quadrigemia* Suffr. and St. John's wort, *Hypericum perforatum* L.

Status of observer	No. of observers	No. of sites
Inspector of Lands (State Government)	16	47
Noxious Weeds Inspector (Local Government)	15	37
Private Landholder	5	11
Entomologist (Federal Government)	2	10
National Park Ranger	1	3
TOTAL	39	108

Some of the sites were chosen by CSIRO officers, including four in which regular, detailed observations on *C. quadrigemina* and St. John's wort population dynamics are being made. The majority, however, were chosen by the observers, who had been asked to select sites which were 'typical' areas of infestation in their respective districts or properties. Thus sites were not chosen because they carried particularly dense or intractable infestations, nor was the presence or absence of *C. quadrigemina* a criterion. Rather, they represented a range of the conditions under which St. John's wort was considered a problem weed. Furthermore, no conditions were placed on the subsequent usage or treatment of sites since it was intended to study the impact of the beetle under normal management practices. Prior to the start of the survey virtually all sites were visited by CSIRO officers to ensure their suitability and to brief observers on the aims and requirements of the survey. The collection of data commenced in the spring of 1982, although some information concerning events in the winter of 1982 had been obtained during the above-mentioned visits.

The survey consists of three separate questionnaires which are sent out to observers at those times of the year which are critical to the life cycle of *C. quadrigemina*: autumn, when adults emerge from aestivation to mate and commence oviposition; winter, when larvae feed on the prostrate growth of St. John's wort; and spring, when new adults emerge and feed on the upright flowering stems. No data is sought in summer when adult beetles aestivate.

The questionnaires seek information in three areas: (1) details of the St. John's wort infestation; (2) the size of *C. quadrigemina* populations and damage caused by them; and (3) management practices used at the site. In addition, information on climatic and physical variables that possibly influence the system is being obtained from other sources (Table 2). Some fine tuning of the questionnaire format, including the addition of some extra questions, was made during the first few surveys. The final format is shown in Appendix 2.

Table 2. Types of data being collected in the survey on the long-term relationship between *Chrysolina quadrigemina* Suffr. and St. John's wort, *Hypericum perforatum* L. in southeastern Australia.

Data Collected	Form of Data	Rating Scale
A. Details of the St. John's wort infestation		
1. Size of infestation being obseved	quantitative	n.a.
2. Density	semi-quantitative	1-3
3. Change in density or size from previous year	semi-quantitative	-2 to +2
4. Plant vigour	semi-quantitive	0-10
5. Extent of infestation beyond plot borders	qualitative	n.a.
6. Amount of tree cover	semi-quantitative	0-2
B. Details of *C. quadrigemina* population and damage caused.		
1. Presence of various life stages in autumn	presence/absence	0 or 1
2. Combined population density/damage rating of adults in spring	semi-quantitative	0-5
3. Combined population density/damage rating of larvae in winter	semi-quantitative	0-5
4. Degree of plant regeneration following defoliation	semi-quantitative	0-10
C. Management practices		
1. Other methods of control used	qualitative	n.a.
2. Grazing pressure and type of stock	qualitative	n.a.
3. Density of other vegetation	semi-quantitative	1-3
D. Other factors potentially important to the system.		
1. Rainfall	quantitative	n.a.
2. Temperature	quantitative	n.a.
3. Soil type	qualitative	n.a.
4. Site position (aspect and slope)	qualitative	n.a.

With regard to the data sought by questionnaire, the observers are asked to indicate which of a number of rating levels or categories best fit the particular sites, using a 'tick the appropriate box' format (see Appendix 2). *C. quadrigemina* is particularly suited to such a system, for the high visibility of adult beetles and of the damage caused by adults and by larvae means that rating levels could be defined which are readily distinguishable. For example, six such categories are used in the critical measurements of beetle population density/damage, ranging from 0 (when *C. quadrigemina* could not be found) to 5 (when large feeding fronts defoliated the entire survey plot) (see Appendix

2). These levels are relative to the density of St. John's wort at each site, so that differences in density of the weed between sites are accommodated in the data.

The questionnaires produce a set of semi-quantitative and qualitative data for each site which can readily be encoded onto computer files. This system was preferred to obtaining more exact quantitative data for several reasons. First, it would have been unfair to expect the observers to devote large amounts of time to the collection of this data, when they had undertaken to carry it out in the course of their normal duties. Second, when such a diverse group of people are carrying out measurements, one could not expect that detailed data would be comparable. Third, although the forms were sent out at one time, the actual times of data collection could vary by several weeks between sites, which would again make comparisons of exact information unreliable. The semi-quantitative rating system sacrifices detail for consistency and comparability, since differences between rating levels are sufficient to accommodate variations due to differences between observers and between the times of observation.

Between 94 and 96% of forms have been returned at each survey period. To help maintain interest in the exercise and a high rate of returns, summaries of the data collected during each observation period are produced and forwarded to the observers with the next set of questionnaires. This also provides feedback which may be of some value to the observers in their own work programs.

Early Results

In a survey where data are collected mainly in a semi-quantitative form, it is important to examine the early returns before becoming committed to long-term involvement, to see whether information collected in this manner is amenable to analysis and likely to provide answers to the questions posed.

As indicated in the previous section, the purpose of this survey is twofold: first, to determine the frequency and extent of damaging outbreaks of *C. quadrigemina*; and second, to determine the underlying factors and contributory stresses associated with these events. Although data have only been collected for 2 yrs, early returns indicate that it will be possible to estimate the temporal and spatial patterns of *C. quadrigemina* populations and their impact on St. John's wort. Fig. 3 shows the distribution and frequency of *C. quadrigemina* damage ratings in spring 1982. This was a period of severe drought in southeastern Australia, and the majority of sites (69%) supported low *C. quadrigemina* population levels, which did not cause significant damage to St. John's wort. Only 11% of sites supported damaging population levels of *C. quadrigemina* and these occurred mainly in that part of the weed's range where winter rains are predominant (Fig. 3). A breakdown of data from other survey periods indicate that this pattern, in which *C. quadrigemina* is present at most sites but is ineffective, has persisted (Fig. 4). Furthermore, significantly more sites in the winter rainfall zone than elsewhere reported damaging population levels of the beetle (20.9 *vs.* 10.4% $t_{404} = 7.0$, $P < 0.01$) over all survey periods. This reflects the traditional view that the beetles are less successful in the northern areas where summer rainfall is more important.

Ultimately, the survey will generate a series of profiles showing temporal changes at each site. Fig. 5 provides examples of such profiles, which will eventually include other factors listed in Table 2. They are from two sites in N.S.W. where successful control of St. John's wort has been attributed to *C. quadrigemina* (Coolah Creek and Cassilis) and from four sites where CSIRO is undertaking more detailed studies. A longer period of records was available for these locations. The profiles show how

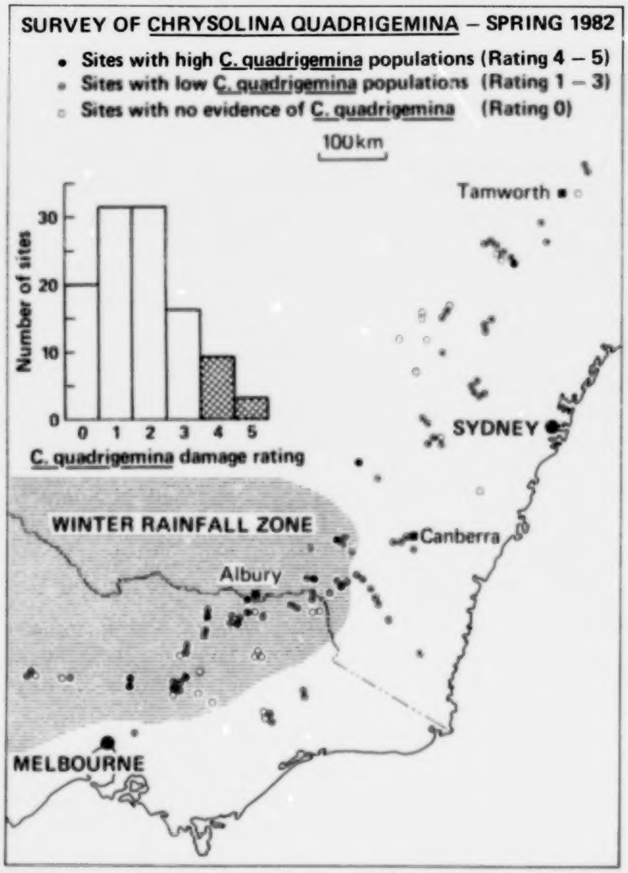
SURVEY OF CHRYSOLINA QUADRIGEMINA – SPRING 1982
Sites with high C. quadrigemina populations (Rating 4 – 5)
Sites with low C. quadrigemina populations (Rating 1 – 3)
Sites with no evidence of C. quadrigemina (Rating 0)
100km
Number of sites
30
20
10
0
0 1 2 3 4 5
C. quadrigemina damage rating
Tamworth
SYDNEY
Canberra
WINTER RAINFALL ZONE
Albury
MELBOURNE

Fig. 3. Pattern and frequency of *Chrysolina quadrigemina* Suffr. populations and associated damage ratings during the spring 1982 survey.

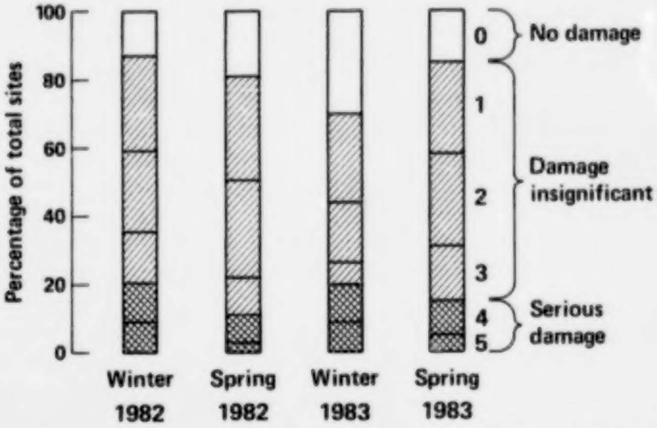

Fig. 4. Percent of sites showing different damage ratings for *Chrysolina quadrigemina* Suffr. over four survey periods.

increases in beetle populations have led to extended declines in the density of St. John's wort at the Coolah Creek and Cassilis sites, followed by a decline in beetle numbers, and finally a resurgence of the weed in 1983 after the breaking of a severe drought. A similar pattern of increase and decline in the beetle population was apparent at Pierce's Creek, but at this site the reduction in St. John's wort density was very transient (Fig. 5). These three sites exhibit the relationship between control agent and host weed shown in Fig. 1*c*. The remaining three sites (Fig. 5) show relationships typical of Fig. 1*b*, in that beetle populations have remained relatively low and have not significantly affected the density of the host weed.

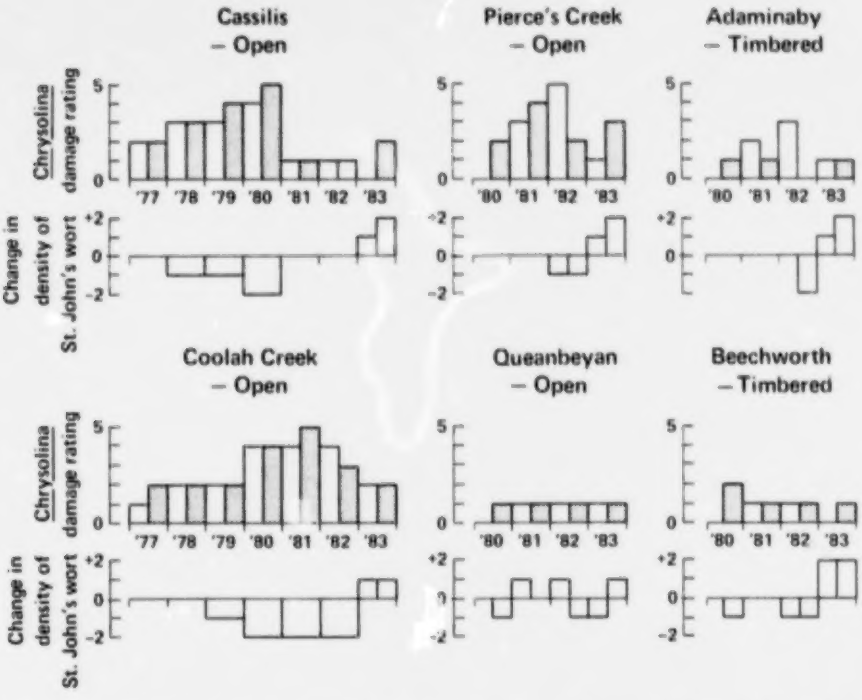

Fig. 5. Temporal patterns of: (a) the damage rating for *Chrysolina quadrigemina* Suffr.; and (b) the change in density of St. John's wort, *Hypericum perforatum* L. at selected sites in southeastern Australia.

The role of contributory factors in the decline of St. John's wort at some sites will have to await the availability of more data. However, the role of the extended drought period from 1980–82 obviously has had some influence. As only a small body of data is available, preliminary analyses have been restricted to the two factors which were considered of prime importance in the revival of the biological control program, namely tree cover and rainfall pattern (Delfosse and Cullen 1981). These suggested that the data being obtained should be able to provide information on the effects of contributory factors.

A comparison of the frequencies of the various damage ratings over all survey periods in 1982–83 showed significant heterogeneity between open sites and those having some tree cover ($X^2_{10} = 37.8$, $P < 0.01$). This was due to the greater incidence of damaging populations in open areas of both larvae in winter and adults in spring (Fig. 6). Such a result was not unexpected, as the aversion of *C. quadrigemina* to heavily shaded areas is well-documented (L.R. Clark 1953). What is important for the survey is that the result indicates that data obtained by a semi-quantitative rating system is capable of identifying such modifying factors.

The proportion of sites with tree cover did not differ significantly between rainfall zones, and therefore did not contribute to the regional differences in the incidence of damaging population levels of *C. quadrigemina* noted earlier. To determine whether rainfall pattern could have influenced this pattern, a series of correlation coefficients and partial correlation coefficients were calculated for several pairs of parameters (Table 3). As one cannot make claims for cause and effect from correlations without corroborating evidence, the following interpretation has been tentatively made, based on information on the biology of *C. quadrigemina* obtained by L.R. Clark (1953).

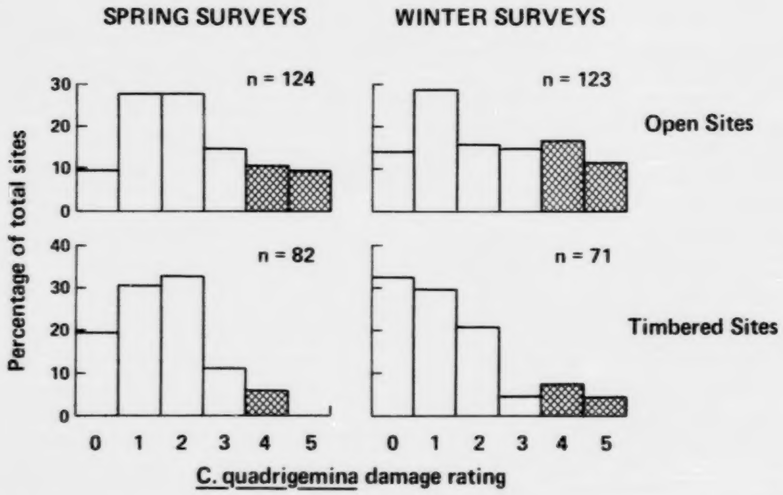

Fig. 6. Influence of tree cover on the frequencies of sites showing different damage ratings for *Chrysolina quadrigemina* Suffr. (hatched bars indicate serious damage).

The occurrence of high population densities of adult *C. quadrigemina* was correlated to winter rainfall in the drought year of 1982–83 and when rains were generally above average in 1983–84 (correlation 1, Table 3). Winter rains promote the growth of procumbent stems of St. John's wort, which provides sufficient food to support a large population of larvae. They also promote the growth of other vegetation which, together with St. John's wort, provides essential shelter for the larvae (L.R. Clark 1953). There was a stronger correlation between larval population density and winter rainfall during 1983–84 than in the preceding drought year (correlation 2, Table 3). Nonetheless, larval populations were able to reduce significantly the density of the weed under drought conditions and when winter rain was favourable (correlation 3, Table 3). Following the onset of above average rainfall during 1983–84 there was a widespread resurgence of St. John's wort, which resulted in a lack of correlation between weed density and winter rainfall for this period, whereas in the preceding year, drought stress over winter had contributed to the reduction of St. John's wort (correlation 4, Table 3). Larvae at more severely drought-stressed sites tended to defoliate the plants more rapidly because of the poor growth, leading to a negative correlation between rainfall and the larval damage rating (correlation 2, Table 3). However, this caused a reduction in food and shelter and subsequent adult populations were greatly reduced at these sites. This explains the much better correlation between adult density and winter rainfall than between larval density and winter rainfall in 1982–83 (Table 3). Thus, while winter drought may favour the control of St. John's wort in the short-term, in the long-term it inhibits the build-up of beetles to damaging levels.

Large populations of adults were also able to reduce the density of St. John's wort (correlation 5, Table 3), although the modifying effect of summer rainfall on the impact of adults (Huffaker 1966) was apparent (correlation 6, Table 3). At most sites high proportions of defoliated plants (up to 90%) recovered when summer rains fell following attack by *C. quadrigemina*.

Table 3. Correlation coefficients between parameters measuring changes in St. John's wort, *Hypericum perforatum* L., density, *Chrysolina quadrigemina* Suffr. damage ratings and rainfall.

Parameters	Correlation Coefficients 1982-83 (Drought year)	 1983-84 (Above average rainfall)
1. Winter rainfall[1] (a) *vs.* spring damage rating (d)	r_{ad} = 0.33**	r_{ad} = 0.25*
2. Winter rainfall (a) *vs.* winter damage rating for larvae (c)	r_{ac} = -0.10n.s.	r_{ac} = 0.24*
3. Winter damage ratings *vs.* subsequent change for larvae (c) in weed density (e) (winter rainfall held constant)	$r_{ce \cdot a}$ = -0.49**	r_{ce} = -0.38**
4. Winter rainfall (a) *vs.* subsequent change in weed density (e) (larval damage rating held constant)	$r_{ae \cdot c}$ = 0.27*	$r_{ae \cdot c}$ = 0.01n.s.
5. Spring damage rating *vs.* subsequent change in: for adults (d) weed density (f)	r_{df} = -0.37**	Not available
6. Summer rainfall[1] (b) *vs.* subsequent change in weed density (f)	r_{bf} = 0.25*	Not available

* Significant at 5% level, ** significant at 1% level.

[1] Winter rainfall measured between April and September, when *C. quadrigemina* larvae are present and St. John's wort procumbent foliage is growing. Summer rainfall measured between November and January, a period critical for the survival of defoliated St. John's wort plants.

Thus the survey data confirms earlier findings on the influence of rainfall patterns on the *C. quadrigemina*–St. John's wort relationship. Moreover, they emphasize the importance of adequate winter rainfall for the success of the beetle. All sites may receive substantial summer rainfall (averages for December–February range from 102–277 mm). Therefore the risk of regeneration of the weed or of upsetting the synchrony of development in the beetle through summer rains stimulating premature emergence from aestivation is present at all sites. Thus, while the higher incidence of summer rainfall may contribute to the generally low success rate of *C. quadrigemina* in southeastern Australia (Huffaker 1966), the regional differences pointed out earlier may be more an effect of differences in the absolute levels of winter rainfall received.

Finally, it is obvious from the low values of the correlation coefficients that the other factors listed in Table 2 (e.g. grazing pressure, management practice, soil type, vegetation density, etc.) are all contributing to the patterns obtained. The analyses used so far have been very simple. When the survey is completed, the data will be subjected to more sophisticated statistical treatments which should make it possible to indicate which of these other factors are influencing the relationship between *C. quadrigemina* and St. John's wort.

Conclusions

Preliminary analyses of the data indicate that the survey will be able to quantify geographic and temporal trends in the population dynamics of *C. quadrigemina* and St. John's wort, and consequently should be able to answer questions pertinent to the ability of the beetle to control St. John's wort, such as:

1. Are there really regional differences in the impact of *C. quadrigemina* and if so, what are they?
2. Do population cycles of *C. quadrigemina* occur in a periodic or haphazard manner?
3. Is there a general overriding pattern in the impact of *C. quadrigemina*; i.e. is there, as some people suggest, such a thing as a 'good *Chrysolina* year'?
4. What type of fluctuations are there in St. John's wort populations independent of *C. quadrigemina* activity?

The survey should produce a solid body of such information, which in hindsight would have been desirable before any new initiatives in the biological control of St. John's wort were undertaken. However, the data being presently obtained can still serve to guide the development of such programs, rather than relying upon what has largely been an oral history of the species. While it may prove more difficult to determine which contributing factors are important at each site, the preliminary analyses indicate that it is possible. Huffaker (1966) pointed out that the complexity of factors involved makes it very hazardous to try and predict the outcome of *C. quadrigemina* activity at any particular site. The results of this survey should enable such predictions to be made with more confidence.

Finally, as indicated in the introduction, a subsidiary aim of this exercise has been to determine whether surveys such as this might be of general use in evaluating the impact of partially successful biological control agents. In this regard, perhaps the most important result is that data collected in a semi-quantitative form can detect patterns and pinpoint factors that may influence the interaction between agent and weed. Obviously, the use of long-term survey data for any particular agent–weed interaction would have to be considered on its individual merits, but some generalities can be made.

Firstly, if rating systems are employed they will detect only relatively large differences in the various parameters. Consequently, their use would be most relevant for species that respond as in Fig. 1*c*, such as *C. quadrigemina*. Secondly, since the survey relies on 'non-expert' help and is not intended to be labour-intensive, the species in question would need to be highly visible, or else inflict damage that was fairly obvious. Insect defoliators, gall-formers and fungal pathogens are such groups of agents, whereas agents which are less visible or inflict more subtle damage, such as stem-borers, root-hair feeders and sap-suckers, might be less amenable to the development of rating categories, especially if they did not show large population fluctuations. More detailed data could perhaps be collected for such species, but this leads to a trade-off between effort and expertise required and time and money available.

Within these limitations such surveys could provide a relatively cheap and efficient way of obtaining essential information about certian control agent–weed interactions.

Acknowledgments

I would like to thank the people listed in Appendix 1 who have acted as observers for this survey. Permission for officers of the Victorian State Government to participate was given by the Department of Crown Lands and Survey. Thanks are also due to K.R. Pullen who helped to set up the survey, and Dr. R. Morton who provided statistical advice.

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Appendix 1. List of observers participating in the survey on the long-term relationship between *Chrysolina quadrigemina* Suffr. and St. John's wort, *Hypericum perforatum* L.

Observer	Location	Number of sites
A. State government Inspectors of Lands, Victoria (Department of Conservation, Forests and Lands)		
T.K. Barnard	Wodonga	4
L.J. Barton	Corryong	2
L. Broadhurst	Walwa	2
J. Carr	Alexandra	5
J. Corrie	Castlemaine	2
A.J. Dobson	Mansfield	4
T. Fitzpatrick	Swifts Creek	2
J.R. James	Tallangatta	2
A. Johnson	Broadford	2
P. Larkin	Beechworth	4
D.K.Muir	Benalla	3
B.S. Oswald	Stratford	4
J.W. Pollard	Warrandite	1
K.P. Rayner	Maryborough	3
E.C.W. Smith	Wangaratta	4
S.R. Williamson	Bright	3
		47
B. Local government Noxious Weeds Officers, NSW		
C. Austin & D. Baldwin	Upper Macquarie County	6
J. Cherry	Central Northern County	4
R. Connell	Tumbarumba Shire	4
S.W. Dickson	Wingecarribee	1
T. Eaglestone	Cabonne Shire	1
P. Ellison	Tumut Shire	3
J. Fahey	Crookwell Shire	4
W. Forbutt	Young Shire	1
J. Kerrison	Harden Shire	2
T. Reed	Orange City	1
W. Ryan	Midwestern County	6
A.R. Smith	Bega Valley Shire	1
M. Steinhaeuser	Cooma-Monaro Shire	1
C. Webb	Wellington Shire	2
		37
C. Private Landholders		
I.R. Arnott	Coolah Creek, NSW	3
E. Coram	Euchareena, NSW	1
A. McMaster	Cassilis, NSW	3
R. Moxham	Trunkey Creek, NSW	2
J. Nader & G. Reilly	Merriwa, NSW	2
		11
D. Others		
D.T.Briese & K.R. Pullen	CSIRO Division of Entomology, ACT	10
W. Jeffs	Kosciusko National Park, NSW	3
		13
	Grand Total	108

Appendix 2. The questionaires used in the survey of the long-term relationship between *Chrysolina quadrigemina* Suffr. and St. John's wort, *Hypericum perforatum* L.

I. SPRING SURVEY OF ST. JOHN'S WORT CONTROL AGENTS.

A. DETAILS OF THE ST. JOHN'S WORT STAND.

1. Location (give name, plus distance to nearest major town)

....

2. Approximate area of infestation (specify hectares or acres)

....

For the following questions please indicate by a cross which best describes the weed infestation

3. Is the St. John's wort stand in an area that is:
mainly open ☐
lightly timbered ☐
densely timbered ☐

4. This year does the St. John's wort stand consist of:
mainly scattered individual plants ☐
a light infestation (scattered patches with isolated plants interspersed) ☐
a dense infestation (large continuous cover or many dense patches) ☐

5. Since last year's survey, has the infestation:
decreased greatly ☐
decreased slightly ☐
remained about the same ☐
increased slightly ☐
increased greatly ☐

6. a) Is the area containing St. John's wort at present:
ungrazed ☐
lightly grazed ☐
heavily grazed ☐

b) What animals are grazing? ....

7. Is the density of other ground vegetation at the site:
low ☐
moderate ☐
high ☐

8. Are any of the following methods being used this year to control St. John's wort in this particular stand:
chemical herbicide ☐
pasture improvement ☐
mechanical removal ☐
other (please state below) ☐

....

9. What is the average height of stems bearing seedheads?

0 - 10cm ☐
10 - 20cm ☐
20 - 30cm ☐
30 - 40cm ☐
40 - 50cm ☐
50 - 60cm ☐
60 - 70cm ☐
70 - 80cm ☐
80 - 90cm ☐
90 -100cm ☐

10. If large areas of St. John's wort had been defoliated by beetles over winter, what percentage of those plants have regenerated?

..............................%

B. OBSERVATIONS ON *CHRYSOLINA* BEETLES.

11. What was the date this Spring when you first observed *Chrysolina* beetles feeding on St. John's wort? ....

12. Please indicate by a cross which description of the density of beetles and damage caused by them best fits the area being examined. (Examine at least 20 plants before answering this question.) If possible check the area again a few weeks after the initial

Appendix 2. Continued.

observation and indicate the highest rating.

☐0 No sign of beetles; no evidence of feeding damage to St. John's wort stands.

☐1 Beetles present, but only found after searching usually singly; no evidence of significant feeding damage to St. John's wort stands.

☐2 Beetles not very common, but obvious on first observation on the stand, occasionally in small groups of 2-5 per stem; little evidence of feeding damage, leaves chewed but no plants showing complete defoliation.

☐3 Beetles quite common, often up to 10-20 per stem on a few plants; feeding damage visible on some plants, with a few completely defoliated.

☐4 Large numbers of beetles, often over 20 per stem on some plants. Feeding fronts forming; complete defoliation of large sections of the St. John's wort stands, but some areas untouched.

☐5 Very large numbers of beetles, often 30-40 per stem on many plants in extensive feeding fronts; complete defoliation of virtually all the St. John's wort stand.

Date of first inspection ....

Date of follow-up inspection (if made): ....

13. REMARKS

If you have any other remarks to make, these can be placed below, e.g. if you can estimate losses in production due to the presence of St. John's wort, please do so.

If you have observed large populations of *Chrysolina* beetles in any other areas, please indicate the names of the locations below.

II. AUTUMN SURVEY OF ST. JOHN'S WORT CONTROL AGENTS.

A. DETAILS OF THE ST. JOHN'S WORT STAND.

1. Location (give name, plus distance to nearest major town)

....

2. Date of survey ....

3. Approximate area of infestation (specify hectares or acres)

....

4. a) Is the area containing St. John's wort at present: ungrazed ☐
lightly grazed ☐
heavily grazed ☐

b)What animals are grazing? ....

5. Is the density of other ground vegetation at the site: low ☐
moderate ☐
high ☐

6. Since last autumn's survey, has the infestation: decreased greatly ☐
decreased slightly ☐
remained about the same ☐
increased slightly ☐
increased greatly ☐

7. What is the condition of the St. John's wort stems? dead ☐
poor condition ☐
healthy ☐

8. What is the average height of stems bearing seedheads?

0 - 10cm ☐
10 - 20cm ☐
20 - 30cm ☐
30 - 40cm ☐

Appendix 2. Continued.

40 - 50cm ☐
50 - 60cm ☐
60 - 70cm ☐
70 - 80cm ☐
80 - 90cm ☐
90 -100cm ☐

9. If large areas of St. John's wort had been defoliated by beetles last spring, what percentage of those plants have regenerated?
..............................%

B. OBSERVATIONS ON CHRYSOLINA

10. *Chrysolina* beetles are normally not as obvious in autumn as in winter, so it is not possible to have a rating scale. In the space below, please record the number of beetles observed by you during a 5 minute search.
....

Chrysolina eggs are laid in autumn on the prostrate winter growth of St. John's wort. They are 1-2mm long, bright orange in colour and occur singly or in small groups of 2-4.

The larvae of *Chrysolina* are small pink, grey grubs which roll themselves into a ball when disturbed. They also occur in the winter growth of St. John's wort, upon which they feed.

Please check the winter growth of St. John's wort for 5 minutes, and indicate below whether any eggs or larvae were observed.

11. *Chrysolina* eggs present ☐
absent ☐
12. *Chrysolina* larvae present ☐
absent ☐

REMARKS

If you have any other remarks to make, these can be placed below.

III. WINTER SURVEY OF ST. JOHN'S WORT CONTROL AGENTS.

A. DETAILS OF THE ST. JOHN'S WORT STAND.

1. Location ....
2. Date of Survey ....
3. What is the average length of the prostrate winter growth?

0- 5cm ☐
6-10cm ☐
11-15cm ☐
16-20cm ☐
21-25cm ☐
26-30cm ☐
31+ cm ☐

4. Is the density of other ground vegetation at the site: low ☐
moderate ☐
high ☐

B. OBSERVATIONS ON CHRYSOLINA

Chrysolina eggs are found on the prostrate winter growth of St. John's wort. They are 1-2mm long, bright orange in colour and occur singly or in small groups.

The larvae of *Chrysolina* are small pink, grey grubs which roll themselves into a ball when disturbed. They also occur on the winter growth of St. John's wort, upon which they feed.

Please check the winter growth of St. John's wort for 5 minutes, and indicate whether any eggs or larvae were observed.

5. *Chrysolina* eggs present ☐
absent ☐

Appendix 2. Continued.

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6. *Chrysolina* larvae present ☐
absent ☐

The larvae of *Chrysolina* feed on the winter growth, eventually leaving only the bare stems remaining. Examine the winter growth in the survey plot for damage by *Chrysolina* and indicate the rating below which best describes what you see.

7. 0 - No signs of feeding damage on winter growth ☐

1 - Signs of feeding on leaves, but *no* plants completely eaten ☐

2 - Feeding obvious, a few plants completely eaten ☐

3 - Large patches of winter growth eaten (up to 50% of plants) ☐

4 - Most winter growth eaten (more than 50%), but some plants remaining ☐

5 - All winter growth completely eaten ☐

REMARKS

If you have any other remarks to make, these can be placed below.

Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 709-20 (1985)

Host-Specificity Studies of the Argentine Weevil, *Heilipodus ventralis*, for the Biological Control of Snakeweeds (*Gutierrezia* spp.) in the U.S.

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Abstract

Snakeweeds (*Gutierrezia* spp.) are troublesome native weeds in rangelands of southwestern U.S. and northern Mexico. The plants impede livestock production by competing with forage plants, and their leaves are poisonous to cattle. The genus originated in North America but seven species also are native in Argentina and five in Chile. Explorations for natural enemies in Argentina showed that the root-boring weevil, *Heilipodus ventralis*, has potential for biocontrol. Its host-plant range was investigated in the field and in the laboratory. In the field, more than 4000 plants in 22 different genera of Compositae were examined; three genera were natural host plants: *Grindelia*, *Gutierrezia* and occasionally *Baccharis*. In the laboratory, larvae and adults were tested on 66 different plant species; development from egg to adult was obtained on *Solidago* and *Aster* in addition to the natural hosts. The weevil appears to be restricted to the plant family Compositae, tribe Astereae, to which all the mentioned genera belong. Important native Astereae should be tested in quarantine in the U.S. before deciding whether or not the weevil should be released.

Essais de Spécificité d'Hôte du Charançon Argentin *Heilipodus ventralis* en Vue de la Lutte Contre les Gutierrezies (*Gutierrezia* spp.) aux États-Unis

Les gutierrezies (*Gutierrezia* spp.) sont des plantes nuisibles dans les pâturages du sud-ouest des États-Unis et du nord du Mexique d'ou elles sont originaires. Ces plantes entravent la production du bétail étant donné qu'elles font concurrence aux plantes fourragères et que leurs feuilles sont toxiques pour le bétail. Le genre est originaire de l'Amérique du Nord, mais il existe six espèces indigènes d'Argentine et cinq espèces indigènes du Chili. En Argentine, parmi les ennemis naturels de cette plante qui ont fait l'objet d'études, le charançon rhizophage *Heilipodus ventralis* semble avoir du potentiel comme agent biologique. Les chercheurs ont étudié la gamme de plantes hôtes de cet insecte sur le terrain et en laboratoire. Sur le terrain, plus de 4000 plantes de 22 genres différents de Composées ont été examinées; trois genres étaient des plantes hôtes naturelles: *Grindelia*, *Gutierrezia* et, parfois, *Baccharis*. En laboratoire, des essais ont été effectués avec les larves et les adultes de cet insecte sur 57 espèces de plantes; outre les hôtes naturels, *Solidago* et *Aster* ont favorisé la croissance des insectes depuis la ponte jusqu'au stade adulte. Le charançon semble se limiter aux hôtes de la famille des Composées, de la tribu des Astérées, auxquelles appartiennent tous les genres mentionnés ci-dessus. Il faudrait procéder à des essais en quarantaine de l'insecte sur les Astérées indigènes les plus répardues aux Etats-Unis avant de décider s'il convient d'introduire le charançon.

Introduction

Snakeweeds (*Gutierrezia* spp.; Campanulales: Compositae) are native weeds in rangelands of the southwestern U.S. and northern Mexico. They have increased greatly in density in the last 100 yrs, mostly because of overgrazing. The plants impede livestock production by competing with forage plants and their leaves are poisonous to cattle.

The genus originated in North America where 16 species occur, 10 in the U.S. (Lane *in press*) but 12 native species also occur in South America: seven in Argentina and five in Chile, all perennials (Solbrig 1966; Cabrera 1971).

Control by conventional chemical and mechanical methods is not applied extensively by ranchers because it is relatively expensive. Biological control by the introduction of foreign natural enemies appears to be an economical alternative. However, most previous attempts on biological control of weeds have been directed against introduced weeds, and therefore, there are only a few records of native weeds controlled by exotic organisms. Only one such case resulted from planned introductions. Nonetheless, there are about 25 documented cases of native insects successfully controlled by exotic natural enemies collected on an allied species or genus. The reason for this success may be the lack of host-natural enemy ecological homeostasis in the new association (Pimentel 1963). Thus, the possibility of controlling the native snakeweeds exists because extensive explorations on the Argentine snakeweeds showed that there are at least seven different species of insects with potential for biological control (Cordo and DeLoach, unpubl. data).*

The host range studies of one of these top candidates, the root weevil *Heilipodus ventralis* Kuschel (Coleoptera: Curculionidae), are discussed here.

The genus *Heilipodus*, with 114 neotropical species, was separated from the genus *Heilipus* by Kuschel (1955). Host plants are known for nine species but precise references are given for only four species which develop inside stems and roots of Umbelliferae (*Eryngium* spp.), Solanaceae (*Capsicum pendulum* Willd.), and Compositae (*Vernonia polyanthes* Less.). The remaining five references are records of adults feeding on buds or resting on the foliage of host plants in eight plant families and with little evidence of association with any particular family. In Brazil, the adults of *Heilipodus clavipes* Fabricius and *H. ocellatus* Olivier are mentioned as pests of cacao, but the larval host plant is unknown (Costa Lima 1968).

The genus occurs from Mexico to Argentina but no species occur in the U.S. In Argentina, 14 species are recorded. *H. ventralis* is known from Paraguay (G. Kuschel, pers. comm.) and Argentina (Blackwelder 1957) but no reference in the literature regarding its host plant was found.

Materials and Methods

Field Host Range

The natural host range of *H. ventralis* in Argentina was explored during several trips made in 1981–84, throughout the area of distribution of *Gutierrezia* spp. Since in Patagonia, *Grindelia chiloensis* (Corn.) Cabr. (Campanulales: Compositae) was about equal to *Gutierrezia* spp. as a host, the area of distribution of *Grindelia* spp. was also surveyed. This area included most of the arid and semi-arid regions of the country, from the northwestern and western provinces to Patagonia. At each exploration point, most recognizable shrubby and sub-shrubby composite plants were dug and their roots dissected for immatures; they were transferred to artificial diet (Harley and Wilson 1968, modified by adding an amount of powdered *Grindelia* stems equal to the amount of alphacel) or held in the excised roots, depending on the immature's condition, until they reached the adult stage. Adults emerged from these immatures or collected as tenerals were considered as the only true indication for natural host plants.

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*Cordo, H.A., and DeLoach, C.J. Insects and pathogens that attack snakeweeds (*Gutierrezia* spp.) in Argentina. *Ann. Entomol. Soc. Amer.* (in review).

Laboratory Host Range

The potential host range of *H. ventralis* was determined by exposing a series of 66 plants under laboratory conditions to both adults and larvae, separately. The selection criteria and plant species tested were as follows:

Species closely related to *Gutierrezia* and *Grindelia*: Compositae, tribe Vernonieae: *Vernonia fulta* Griseb.; tribe Eupatorieae: *Eupatorium tremulum* H. et A.; tribe Astereae: *Aster novi-belgii* L., *Baccharis darwinii* H. et A., *B. divaricata* Hauman, *B. trimera* (Less.) DC., *Erigeron karvinskianus* DC., *Grindelia buphthalmoides* DC., *G. chiloensis*, *G. pulchella* Dun., *Gutierrezia solbrigii* Cabr., *Solidago chilensis* Meyen; tribe Inuleae: *Inula helenium* L.; tribe Heliantheae: *Dahlia excelsa* Benth., *D. pinnata* Cav., *Helianthus annuus* L., *H. tuberosus* L., *Zinnia elegans* Jacq., *Xanthium cavanillesii* Schouw; tribe Helenieae: *Gaillardia pulchella* var. *picta* (Sweet) Gray, *G. aristata* Pursh, *Hymenoxys robusta* Parker, *Tagetes patula* L., *T. erecta* L.; tribe Anthemideae: *Artemisia absinthium* L., *A. annua* L., *A. drancunculus* L., *A. verlotorum* Lamotte, *Achillea millefolium* L., *A. filipendulina* Lam., *Chrysanthemum carinatum* Schousb., *C. coccineum* Willd., *C. maximum* Ram., *C. parthenium* (L.) Bernh., *C. vulgare* (Lam.) Parsa, *Chrysanthemum* sp.; tribe Senecioneae: *Senecio goldsackii* Ph., *S. cineraria* DC., *S. cruentus* DC., *S. mikanioides* Otto, *S. petasitis* DC.; tribe Cynareae: *Carthamus tinctorius* L., *Centaurea dubia* Suter, *Carduus nutans* L., *Cynara cardunculus* L., *C. scolymus* L.; tribe Mutisieae: *Mutisia retusa* Remy; tribe Cichorieae: *Cichorium intybus* L., *Lactuca sativa* L.

Families, genera, or species attacked by insects of the genus *Heilipodus*: Bromeliaceae: *Ananas comosus* (L.) Merrill, *Bromelia balansae* Mez.; Rosaceae: *Pyrus communis* L.; Vitaceae: *Vitis labruscana* Bailey; Myrtaceae: *Eucalyptus fastigata* Deane & Maiden, *E. kruseana* F.U.M., *Psidium guajava* L.; Umbeliferae: *Eryngium eburneum* Decaisn.; Solanaceae: *Capsicum frutescens* L.

Families, genera, or species attacked by insects of the genus *Heilipus* (*sensu lato*): Moraceae: *Ficus carica* L.; Anonaceae: *Rollinia emarginata* Schlecht.; Lauraceae: *Persea americana* Mill.; Leguminosae: *Glycine max* (L.) Merrill; Aquifoliaceae: *Ilex paraguariensis* Saint Hil.; Malvaceae: *Gossypium hirsutum* L.; Verbenaceae: *Acantholippia seriphioides* (A. Gray) A. Mold., *Aloysia gratissimia* (Gill & Hook.) Troncoso.

Adult testing. Three different types of tests were carried out to determine the ability of *H. ventralis* adults to feed and oviposit on a wide spectrum of plants: a no-choice test of the natural host plants; a multiple-choice test of all 66 test plants; and an oogenesis test. All these tests were done in a 25±3°C cabinet, with fluctuating humidity between 40–70% and 14 h photophase.

The natural host plants were tested for ovipositional preference in a no-choice test to determine if biotypes of the weevil exist. Insects from inside the roots of *G. chiloensis* and *G. solbrigii* were collected as pupae at San Antonio Oeste, Rio Negro Province, 12 November 1982, and as ready-to-emerge adults at Arroyito, Neuquen Province, 7–9 December 1982, respectively. Newly emerged adults from both populations were fed separately with *G. solbrigii*, *G. chiloensis*, and *G. pulchella*, totalling 6 treatments which were repeated 10 times. Each replication consisted of 2 adults (1 male and 1 female) placed in a glass cylinder 12 × 12 cm diam., half-filled with moist peat moss and covered with nylon cloth to confine the insects. The food plant was prepared as a bouquet in a small vial filled with water and buried in the peat moss. For oviposition, 2 or 3 woody stems of *G. pulchella* about 7 mm diam. × 70 mm long, were stuck half-way in the peat moss. Stems of *G. pulchella* were used for all treatments because this plant was locally available, and therefore, the only one able to supply the large number of stems needed. Twice a week the terminal buds and the stems for oviposition were replaced by fresh material and the eggs collected from the renewed stems placed in 1 oz cups with agar gel plus antimicrobials for hatching; the test started 13–20 December 1982 and ended July 1983, when all the adults died.

All test plants were compared in 2 multiple-choice tests of feeding and oviposition. A total of 65 different plants were exposed to a total of 230 adults from diverse origins. Each testing unit consisted of 10 adults (5 males and 5 females, not fed for 24 h) placed in a plastic tray with moist peat moss at the bottom, where pieces of stems for oviposition were introduced, contiguous to terminal buds for feeding. Two stems (2–5 mm diam. × 50 mm long, woody whenever possible) and 2 terminal buds 50 mm long of each plant were placed at opposite locations of the tray, which was covered with a clear polyethylene film. The adults were released in the center of the tray. After the test, the stems were dissected for collection of eggs and the terminal buds were examined for evidence of feeding. The amount of feeding was calculated by measuring the volume of both leaves and stems consumed. In the leaves, the area of the feeding hole was measured with a millimetric grid; that area multiplied by the thickness of the leaf gave the volume consumed. In the stems, the total volume of the partially damaged segment was measured and from that volume the proportion consumed was estimated visually. Using the described methodology, most of the plants were exposed to the attack of 10 adults, 12–14 times. Two different populations of *H. ventralis* were tested with slight variation in the methods as follows:

Test A. Insects were collected as adults on *Grindelia chiloensis* and *Gutierrezia solbrigii* in several eastern sites of Chubut and Rio Negro Provinces in Patagonia, 13–16 January 1983. Estimated age at beginning of test was 1–2 months. Fifteen testing units were set: 5 containing the 28 chosen test plants plus the natural host plants; 5 with the 28 chosen test plants without the natural host plants; and 5 with the natural host plants only. In this way, every plant was equally exposed to the attack of 100 adults total. Duration of the test was 72 h.

Test B. Insects were collected as larvae inside the roots of *G. chiloensis*, near Chelforo, Rio Negro in northern Patagonia, 21 February 1982. They were reared on artificial diet until emergence of adults on September 1982 and fed on *G. chiloensis* until their use, about one month later. Four pairs of testing units were set at different times, according to adult availability. Each pair consisted of 1 tray (35 × 25 × 8 cm) containing the chosen test plants (about 10–15) plus the natural host plants, and another tray with the chosen test plants only. Examination for eggs and feeding was done 48 h after beginning the test.

An oogenesis test was conducted to determine if potentially suitable host plants (as found in previous tests) in the tribe Astereae, like *Aster* and *Solidago*, were appropriate for maturation of oocytes when newly emerged adults fed exclusively on these plants. Other plant species were also tested for comparison. *Gutierrezia* was not included because sufficient plants were not available at the time. It is important to remark that since stems for oviposition used for all the test plants were of *G. pulchella*, this test was intended to determine the nutritional suitability of the tested plants, rather than their total potentiality.

Adults used for the oogenesis test were collected as larvae inside the roots of *G. solbrigii* and *G. chiloensis* at San Antonio Oeste, Rio Negro Province, 15 September 1983 and reared on artificial diet. Each test plant was exposed to 2 newly emerged adults (1 male and 1 female), using the same technique described for the natural host preference test, and repeated 10 times.

Larval testing. This test was conducted using plants of the Compositae because previous tests suggested that the best chances to detect potential host plants were among members of that family. Larvae were obtained from eggs laid in the laboratory by insects collected as adults on *G. solbrigii* and *G. chiloensis* in Chubut and Rio Negro, 13–16 January 1983. One neonate larva was placed in each of 3 holes in the stems of each test plant. The holes were made with a 2 mm drill in the crown or in the stem up to 5–8 cm above the crown. Ten replications of each test plant were made, i.e. each plant species was exposed to 30 larvae of *H. ventralis*. After the larvae were inserted, the hole was sealed with teflon tape and an adhesive plastic tape covering it for protection. When the larvae were placed in the crown or below (because stems were too thin), the hole was plugged with solid paraffin and then sealed with melted paraffin. Plants used were growing in pots inside an open insectary, except for *C. tinctorius*, *H. annuus*, and *C. intybus* which were growing in the ground. One month after the beginning of the test, the first replication of each test plant was dissected for evidence of larval survival. If the 3 larvae were found dead, then the second replication was examined and so on, until the first living larva was found; at this point, the surviving larva was transferred to a new plant. This operation was repeated at the second, third, fourth, and seventh month to record larval mortality. The test started in February 1983 (summer) and continued until all surviving adults had emerged 10 months later in December (spring). During the winter months, the insectary sides were closed with clear polyethylene and slightly heated; the temperature for that period was mean minimum 11°C and mean maximum 25°C.

Results and Discussion

Adults of *H. ventralis* are brownish, mottled with white, about 11 mm long by 4 mm wide. They fed mostly on the tender stem tissues at the tip of the *Grindelia* spp. plants, but on *Gutierrezia* spp. (where the terminal stems are very thin and not succulent as in *Grindelia*) they fed mostly on the sap by clipping off buds and leaves. Laboratory potted plants were killed by this feeding, but no evidence of similar heavy damage was observed in the field. Females oviposited in the summer. A female bored a hole in the crown with her rostrum, in which she laid a single egg. Females produced about 100 eggs during their lifetime. Larvae tunneled in the crown and taproot, where usually several were found together. Larvae pupated in roots in early spring. In late spring, adults emerged by making a hole through the pupation cell with their mandibles. There was only one generation/yr.

Field Host Range

Among the 4076 composite plants examined in the field, which included 7 tribes, 22 genera and 45 species, 12 species were found as larval host plants of *H. ventralis* (Table 1). These species are in the genera *Grindelia*, *Gutierrezia*, and *Baccharis*, all in the tribe Astereae and all shrubby or sub-shrubby plants, except for *B. pingraea* DC. which is a perennial herb. The number of insects found and the proportion of plants damaged at each site surveyed were definitely greater for *Grindelia* spp. and *Gutierrezia* spp. than for *Baccharis* spp. Adult feeding was easily detected on the tips of *Grindelia* spp., whereas it was unnoticed on *Gutierrezia* spp. and *Baccharis* spp. *Solidago* was surveyed only once, in spite of the large distribution of *S. chilensis* in the country,

Table 1. List of Compositae dissected in the field to determine the natural host range of *Heilipodus ventralis* Kuschel in Argentina.

Plants dissected	***H. ventralis***			
	No. sites surveyed	No. plants dissected	No. sites where found	No. insects found[1]
Tribe Vernonieae				
Vernonia nitidula Less.	1	5	0	0
Tribe Eupatorieae				
Eupatorium patens Don (H. et A.)	1	8	0	0
Tribe Astereae				
Baccharis articulata Pers.	3	45	2	+
B. boliviensis Cabr.	2	30	0	0
B. crispa Spreng.	2	63	2	+
B. darwinii H. et A.	13	145	1	+
B. divaricata Hauman	1	30	1	+
B. pingraea DC.	3	62	2	+
B. salicifolia Persoon	2	10	0	0
B. trimera (Less.) DC.	1	5	0	0
B. ulicina H. et A.	4	35	0	0
Baccharis spp. (X 2)	5	41	3	+
Grindelia buphthalmoides DC.	1	20	0	0
G. cabrerae Ariza	1	6	0	0
G. chiloensis (Corn.) Cabr.	19	610	17	+ + +
G. pulchella Dun.	28	729	13	+ + +
G. tehuelches Cabr.	6	101	5	+ +
Gutierrezia gilliesii Gris.	9	266	4	+ +
G. mandonii Solbr.	3	170	0	0
G. solbrigii Cabr.	17	592	16	+ + +
G. spathulata Kurtz	4	265	3	+ + +
Solidago chilensis Meyen	1	20	0	0
Heterothalamus sp.	1	40	0	0
Tribe Heliantheae				
Flourensia sp.	3	20	0	0
Helianthus sp.	1	25	0	0
Parthenium sp.	1	15	0	0
Thelesperma megapotamica OK.	1	10	0	0
Zinnia peruviana L.	1	10	0	0
Tribe Helenieae				
Gaillardia megapotamica (Spreng.) Baker in Martius	1	10	0	0
Helenium alternifolium Cabr.	1	10	0	0
Schkuhria pinnata OK.	1	33	0	0
Thymophylla belenidium Cabr.	1	10	0	0
Tribe Senecioneae				
Senecio filaginoides DC.	9	151	0	0
S. goldsackii Ph.	2	40	0	0
S. hyeronymi Gris.	1	50	0	0
S. schreiteri Cabr.	2	150	0	0
S. subulatus Don.	1	10	0	0
S. viridis Phil.	1	50	0	0
Senecio sp.	6	74	0	0

Table 1. Continued.

Plants dissected	*H. ventralis* No. sites surveyed	No. plants dissected	No. sites where found	No. insects found[1]
Tribe Mutisieae				
Aphyllocladus spartioides Weld.	1	15	0	0
Brachyclados hycioides Don.	1	15	0	0
Chuquiraga avellanedae Lor.	1	30	0	0
Hyalis argentea Don. var. *latisquama* Cabr.	1	30	0	0
Trichocline plicata H. et A.	1	10	0	0
T. reptans Rob.	1	10	0	0

[1] + : less than 10
++ : 10 to 50
+++ : more than 100

because it occurs only in more humid areas where *H. ventralis* is not present. Although the genus *Aster* has about 14 species in Argentina, no species of Aster were found at the sites surveyed.

Laboratory Testing

Adult testing. A test was conducted to determine if reproduction differences between two weevil populations from Patagonia, one from *Gutierrezia solbrigii* and one from *Grindelia chiloensis*, might indicate different biotypes of the weevil on different host plant genera. Survival, preoviposition period, and total eggs/female were not different, therefore providing no evidence for the existence of biotypes.

When field-collected adults were offered 66 plant species in 14 different families, in a multiple-choice test, weevils showed a marked preference to feed and oviposit on the composites, particularly those in the tribe Astereae (Table 2). In fact, they laid all the eggs on members of that tribe, except for 3 eggs laid on *Artemisia annua*. Of the 99 eggs laid, 89 were laid on plants previously determined as natural hosts. Therefore, feeding or oviposition on plants other than the field hosts were relevant only on *Aster*, *Solidago*, and *Artemisia* and consequently, further testing was necessary for these plants. No consistent differences were seen between Test A where the adults were collected from the field from both *Grindelia* and *Gutierrezia* and Test B where the adults were reared from larvae collected in the field only in *Grindelia*.

When newly emerged, immature adults were fed with *Aster*, *Solidago*, and *Artemisia* (*A. verlotorum* was tested because *A. annua* was not available) as a sole source of food, only *Aster* proved to be nutritionally adequate to induce oocyte maturation (Table 3). Feeding and fertile eggs were produced on every plant of the test, but these results are meaningful only when the test plants are compared with the control of *G. chiloensis*. A clear-cut difference was seen between *G. chiloensis*, *G. buphthalmoides*, and *A. novi-belgii* and the rest of the plants. Feeding, number of eggs laid, and survival were larger in the first group, than in the second group. Also, in the first group the number of eggs laid were proportional to the amount of food consumed, and no eggs were laid before beginning of feeding. In the second group, the number of fertile eggs/female varied from 1 to 3, showing no relationship with the amount of food consumed. For

Table 2. Feeding and ovipositional preferences of *Heilipodus ventralis* Kuschel adults on plants of different families in two multiple choice tests[1]

Test plants	Total		
	Feeding (mm^3)	No. eggs	No. testing units (10 adults/unit)
Anonaceae			
Rollinia emarginata Schlecht.	2.4	0	12
Leguminosae			
Glycine max (L.) Merrill	6.5	0	10
Aquifoliaceae			
Ilex paraguarensis Saint Hil.	2	0	12
Vitaceae			
Vitis labruscana Bailey	1	0	12
Myrtaceae			
Psidium guajaba L.	1.5	0	14
Solanaceae			
Capsicum frutenscens L.	7.7	0	14
Compositae			
Tribe Vernonieae			
Vernonia fulta Griseb.	5	0	14
Tribe Astereae			
Aster novi-belgii L.	212	3	14
Baccharis darwinii H. et A.	15	0	13
B. divaricata Hauman	300.7	2	14
B. trimera (Less.) DC.	47.4	7	16
Erigeron karvinskianus DC.	6.3	0	14
Grindelia buphthalmoides DC.	1486	4	13
G. chiloensis Cabr.	3073.5	14	14
G. pulchella Dun.	1043	33	14
Gutierrezia solbrigii Cabr.	704	29	14
Solidago chilensis Baker	518.5	4	14
Tribe Heliantheae			
Dahlia excelsa Benth.	4	0	14
Helianthus annuus L.	2.2	0	14
H. tuberosus L.	0.7	0	14
Tribe Helenieae			
Gaillardia aristata Pursh.	3.4	0	14
G. pulchella var. *picta* (Sweet) Gray	40	0	14
Tagetes patula L.	11.5	0	14
Tribe Anthemidae			
Artemisia absinthium L.	15	0	14
A. annua L.	57.5	3	12
A. dracunculus L.	13.3	0	14
A. verlotorum Lamotte	5.4	0	14
Chrysanthemum carinatum Schousb.	4	0	4
C. coccineum Willd.	8.6	0	14

Table 2. Continued.

Test plants	Total		
	Feeding (mm^3)	No. eggs	No. testing units (10 adults/unit)
C. parthenium (L.) Bernh.	50	0	4
Tribe Senecioneae			
Senecio cruentus (Mass.) DC.	4	0	4
S. mikanioides Otto	0.4	0	2
Tribe Cynareae			
Carduus nutans L.	6	0	12
Carthamus tinctorius L.	15.8	0	14
Cynara cardunculus L.	11	0	14
Tribe Mutisiae			
Mutisia retusa Remy	1.4	0	10
Tribe Cichorieae			
Cichorium intybus L.	2.2	0	14

[1] The plants showing neither feeding nor eggs are not included in the table. These are: *Ananas comosus* (L.) Merrill, *Bromelia balansae* Mez., *Ficus carica* L., *Persea americana* Mill., *Pyrus communis* L., *Gossypium hirsutum* L., *Eucalyptus fastigata* Deane and Maiden, *E. kruseana* F.U.M., *Eryngium eburneum* Decaisn., *Acantholippia seriphioides* (A. Gray) A. Mold., *Aloysia gratissima* (Gill & Hook.) Troncoso, *Eupatorium tremulum* H. et A., *Inula helenium* L., *Dahlia pinnata* Cav., *Zinnia elegans* Jacq., *Xanthium cavanillesii* Schoum., *Hymenoxys robusta* Parker, *Tagetes erecta* L., *Achillea millefolium* L., *A. filipendulina* Lam., *Chrysanthemum* sp., *C. maximum* Ram., *C. vulgare* (L.) Bernh., *Senecio goldsackii* Ph., *S. cineraria* DC., *S. petasitis* DC., *Cynara scolymus* L., *Lactuca sativa* L.

example, adults that consumed 44.5 mm^3 of *Solidago* laid about equal numbers of fertile eggs/female as did adults placed on *B. darwinii* that did not feed; adults fed on *Artemisia* and *Lactuca* laid 4 and 18 fertile eggs, respectively, before feeding started. Therefore, females were able to lay fertile eggs before any food was consumed. Many of the eggs laid in the second group of plants in Table 3 were laid before females began feeding, and thus are not associated with nutritive quality of the food plant.

Larval testing. Further testing of larvae on different Compositae showed that larval development occurred only among members of the tribe Astereae; adults were produced on the natural host plants plus *Aster* and *Solidago* (Table 4). Mortality during the first instar was high for all the plants, but lesser in the Astereae (72.6%) than in the remaining plants (95.0%), where no larvae reached the fourth instar.

Conclusions

It can be safely assumed that the host range of *H. ventralis* is restricted to the plant family Compositae, tribe Astereae. Extensive field explorations in most of the weevil's distribution area showed that its natural host plants are species of *Grindelia*, *Gutierrezia*, and occasionally *Baccharis*. No explorations were done in Paraguay where the insect also occurs, but the preference of *H. ventralis* for arid situations in Argentina suggests that probably the insect populations in the subtropical climate of Paraguay would be low.

Although adult feeding preferences for *Grindelia*, then *Gutierrezia*, and last *Baccharis* were detected in the field and observed in the laboratory, we found no evidence for the existence of sibling species. Two populations tested, occurring on different host plants and from different locations, showed about equal reproductive parameters. Previous observations not reported here also proved that insects of *Grindelia* and *Gutierrezia* from different sites interbred freely. Laboratory studies to determine the potential host range indicated that the genera *Aster* and *Solidago* could serve as host plants if certain ecological conditions are met. These two genera were not surveyed much in Argentina for two reasons: first, they usually do not coexist with the normal host plants because they prefer more humid habitats and second, most Argentine species of both genera are perennial herbs in contrast to the sub-shrubby and shrubby form of the normal host plants. Therefore, there is little chance that *Aster* and *Solidago* are natural hosts of *H. ventralis* in Argentina.

Table 3. Oviposition, feeding and survival of *Heilipodus ventralis* Kuschel adults during their entire life when fed exclusively on certain Compositae[1]

	Feeding (mm^3)	Number of eggs laid per female				Female survival (days)
				Laid before beginning of feeding		
Test plants	Total/adult	Total	Fertile	Total	Fertile	
Tribe Astereae						
Grindelia chiloensis Cabr.	1157.5 *a*	51.1 *a*	38.7 *a*	0	0	86.7 *a*
G. buphthalmoides DC.	984.6 *b*	38.4 *b*	20.5 *b*	0	0	83.7 *a*
Aster novi-belgii L.	252.2 *c*	14.0 *c*	8.5 *c*	0	0	81.3 *a*
Solidago chilensis Baker	44.5 *d*	2.4 *d*	1.5 *d*	0	0	52.7 *bc*
Baccharis trimera (Less.) DC.	7.8 *d*	3.9 *d*	1.8 *d*	1	0	53.6 *bc*
B. darwinii H. et A.	0 *d*	3.3 *d*	1.4 *d*	3.3	1.4	39.4 *de*
Tribe Heliantheae						
Helianthus tuberosus L.	12.8 *d*	4.4 *d*	3.0 *d*	0	0	50.9 *bc*
Tribe Anthemideae						
Artemisia verlotorum Lamotte	21.3 *d*	2.9 *d*	1.0 *d*	1.4	0.4	32.0 *e*
Tribe Cynareae						
Centaurea dubia Cabr.	19.2 *d*	4.5 *d*	2.9 *d*	0	0	57.5 *b*
Tribe Cichorieae						
Latuca sativa L.	5.8 *d*	4.5 *d*	1.8 *d*	4.1	1.8	46.5 *cd*

[1] Numbers are means of 10 replications. Same letter means non-statistical difference at 1% level (Duncan's test).

In regard to both the natural and potential host range of *H. ventralis*, a distinction should be made between adult and larval host range. Adult host range seems narrower and restricted to *Grindelia*, *Gutierrezia*, and to a minor extent *Aster*, the 'perfectus' host plants that are able to sustain the development and maturation of larvae and adults. Regarding larval host range, the results of the oogenesis and larval survival tests suggest that species in the genera *Baccharis* and *Solidago* could be considered as 'imperfectus' host plants, because they are nutritionally adequate for larval development but not for adult oogenesis. Therefore, they probably would be occasional host plants as the paucity of *H. ventralis* found on *Baccharis* spp. seems to indicate.

Table 4. Survival of 30 larvae of *Heilipodus ventralis* Kuschel placed in crowns or stems of each species of certain Compositae.

Test plants	No. of larvae found dead in instar I	II	III	IV	V-VIII	Adults emerged
Tribe Vernonieae						
Vernonia fulta Griseb.	30	0	0	0	0	0
Tribe Astereae						
Aster novi-belgii L.	24	1	4	0	0	1
Baccharis darwinii H. et A.	30	0	0	0	0	0
Erigeron karvinskianus DC.	28	1	1	0	0	0
Grindelia chiloensis Cabr.	12	4	4	3	0	7
G. pulchella Dun.	20	0	0	8	0	2
Guterrezia solbrigii Cabr.	20	0	5	2	0	3
Solidago chilensis Baker	20	4	2	2	0	2
Tribe Heliantheae						
Dahlia sp.	30	0	0	0	0	0
Helianthus annuus L.	29	1	0	0	0	0
H. tuberosus L.	28	1	1	0	0	0
Xanthium cavanillesii Schoum.	30	0	0	0	0	0
Zinnia elegans Jacq.	29	1	0	0	0	0
Tribe Helenieae						
Gaillardia pulchella var. *picta* (Sweet) Gray	28	1	1	0	0	0
Tagetes patula L.	27	2	1	0	0	0
Tribe Anthemideae						
Achillea filipendulina Lam.	29	0	1	0	0	0
Artemisia verlotorum Lamotte	24	3	3	0	0	0
Chrysanthemum maximum Ram.	29	1	0	0	0	0
Tribe Senecioneae						
Senecio cineraria DC.	29	1	0	0	0	0
Tribe Cynareae						
Carthamus tinctorius L.	30	0	0	0	0	0
Centaurea dubia Carb.	23	2	5	0	0	0
Cynara cardunculus L.	30	0	0	0	0	0
Tribe Mutisiae						
Mutisia retusa Remy	30	0	0	0	0	0
Tribe Cichorieae						
Cichorium intybus L.	29	1	0	0	0	0

The tribe Astereae is better represented in the northern than in the southern hemisphere. The genera *Grindelia, Gutierrezia, Aster,* and *Baccharis* have several to many species native in North America, and the risks of a foreign insect attacking them must be assessed before any introductions are made. For this reason it is recommended that important native Astereae should be tested in quarantine in the U.S. before deciding whether or not the weevil should be released.

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Biology and Impact of *Trichobaris texana* (Coleoptera: Curculionidae) on Silverleaf Nightshade, *Solanum elaeagnifolium* in Central Texas*

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Abstract

The biology of the curculionid *Trichobaris texana* was investigated in Brazos County, Texas. Females oviposit in leaf midribs and petioles of silverleaf nightshade, *Solanum elaeagnifolium*. The incubation period for the eggs averaged 6.2 days in the laboratory. Larvae mined the stem pith of the host plant and completed their development in an average of 56.0 days. Pupation occurred inside the stem in cells of loosely-packed wood fibers constructed by the mature larvae. Duration of the pupal stage averaged 11.1 days. Adults eclosed in the pupal cells and overwintered inside the stems. The temporal distribution of all life stages indicated that *T. texana* is univoltine. Life and fertility tables were constructed from laboratory cohorts to facilitate calculation of basic population statistics; the net reproductive rate (R_o) for *T. texana* was 1.41, the cohort generation time (T_c) was 92.55 days, and the capacity for increase (r_c) was 0.0037. Thus, the population would increase 1.004 times/day, and 187 days would be required for the population to double. The effect of larval feeding on the seasonal rate of growth of silverleaf nightshade was also evaluated. The data suggest that tunneling activity of larvae inside the stems ultimately stunts plant growth.

Biologie de *Trichobaris texana* (Coléoptères: Curculionidés) et ses Effets sur la Morelle *Solanum elaeagnifolium* au Centre du Texas

La biologie de *Trichobaris texana* a été étudiée dans la Brazos County, au Texas. Les femelles pondaient leurs oeufs sur les nervures et les pétioles des feuilles de la morelle *Solanum elaeagnifolium*. En moyenne, la période d'incubation des oeufs était de 6.20 jours en laboratoire. Les larves mineuses pénétraient dans la médule des tiges et le stade larvaire durait, en moyenne, 56.01 jours. La pupation se produisait à l'intérieur de la tige de la plant hôte, dans des cellules de fibres lâches construites par les larves matures. La pupation prenait une moyenne de 11.10 jours. Les adultes éclosaient dans les cellules de la pupe et hibernaient dans les tiges. D'après la répartition temporelle de toutes les étapes de développement de l'insecte, *T. texana* est univoltine. Les tables de survie et de fertilité ont été établies à partir de cohortes élevées en laboratoire afin de faciliter le calcul des statistiques de base relatives aux populations; le taux net de reproduction (R_o) de *T. texana* était de 1.41, la durée entre deux générations de la cohorte (T_c) était de 92.55 jours et la capacité d'augmentation (R_c) était de 0.0037. Par conséquent, la population pourrait augmenter 1.004 fois par jour et ainsi deubler en 187 jours. Les effets de l'alimentation des larves sur le taux saisonnier de croissance de la morelle ont également été évalués. D'après les données, les tunnels creusés par les larves à l'intérieur des tigres entravent la croissance des plantes et entraînent finalement leur rabougrissement.

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Introduction

Silverleaf nightshade (SLN), *Solanum elaeagnifolium* Cav. (Solanaceae), is believed to be native to the United States and Mexico (Goeden 1971) or is perhaps indigenous to South America (Siebert 1975). This weedy solanum occurs across the southwestern United States primarily along roadsides, railroad rights-of-way, and in disturbed but less intensively cultivated areas of irrigated agriculture (Goeden 1971). According to the latter author, SLN was apparently introduced into California *c.* 1890, and by 1965 infested 3200 ha of prime agricultural land in 34 counties.

In addition to its status as a weed, all parts of SLN contain the chemical compound solanine which is toxic to humans and livestock when ingested (Kingsbury 1964). Sperry *et al.* (1977) reported that SLN is the most poisonous solanum in Texas and is frequently the cause of extensive cattle losses.

Recent faunistic surveys of the phytophagous insects associated with SLN and related solanums (Burke 1963; Goeden 1971) revealed that *Trichobaris texana* LeConte (Coleoptera: Curculionidae) (Fig. 1) is an important natural enemy of this weed. All stages of *T. texana* were dissected from visibly weakened SLN plants in south central and southeastern Arizona; the obvious stress in some plants was attributed to the stem boring activity of the larvae (Goeden 1971).

T. texana is found primarily in the southwestern United States, but ranges into Colorado, Kansas, Arkansas, and Mexico (Fig. 2). In addition to SLN, other host plants of *T. texana* are *S. rostratum* Dunal (Barber 1935; Burke 1963), *S. dimidiatum* Raf. (= *S. torreyi* Gray), and *S. citrullifolium* A. Br. (= *S. heterodoxum* Dunal) (Barber 1935). A host plant is defined here as one on which larval development is normally initiated and completed.

The biology of *T. texana*, a potential control agent for SLN, has not been previously studied. This paper presents information on a study that was conducted in Central Texas during the period 1978–79. The primary purpose of this research was to determine the life cycle and ecology of *T. texana* on SLN, and assess the impact of this weevil on its host plant.

Methods and Materials

An established stand of SLN located in a pasture of the Beef Cattle Center at Texas A & M University, College Station, Texas, U.S.A., was selected as the sampling area. Insect and plant populations were sampled periodically from July to September 1978 and then once a week from April to December 1979. The purpose of the 1978 sampling program was to obtain a sufficient number of experimental larvae to develop a successful laboratory rearing procedure and to obtain an ample supply of pupae and teneral adults for laboratory experiments conducted during 1979. To simulate overwintering conditions, stem sections of SLN with adults *in situ* were kept in an incubator maintained at *c.* 4°C from December 1978 to April 1979.

In March 1979, a sampling area was selected which consisted of a *c.* 0.46 ha block (87.5 × 52.5 m) located in the northeast corner of pasture no. 12. The high density of SLN, low probability of extraneous disturbances (e.g. mowing, disking, and herbicide application), and close proximity to the laboratory were the primary criteria for block selection.

The sampling block was divided into 15 plots. Each plot was 306.25 m^2. Samples were collected from each plot on a weekly basis by the stratified random sampling method to minimize the variance between plots (Southwood 1978). The actual sampling site was chosen by using a table of random numbers to select different coordinates for each sampling date within each plot. A sample of 15 plants was obtained on each sampling date (1 plant/plot). Insect population estimates for a given sampling date were reported as the number/plant, which is a measure of population intensity (Southwood 1978).

The destructive and tedious nature of the sampling technique and the limited sampling area were the major factors for restricting sampling to a total of 15 plants/wk.

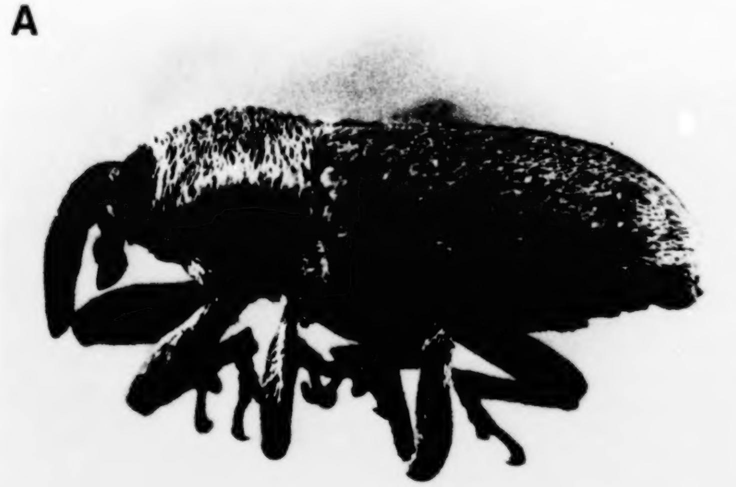

Fig. 1. *Trichobaris texana* LeConte. (A) male; (B) female.

Samples were taken by closing the two halves of a 25 cm diam. circular plywood disk around the base of a plant; the area encircled was then searched quickly for insects that might crawl or fly out of the marked area. The plants were then examined for insects, removed by clipping the stems at ground level with pruning shears, and placed in large plastic bags. The plants were transported to the laboratory for detailed examination.

In the laboratory, host plant growth was monitored by measuring overall height of infested and normal plants. These data were used to determine the impact of the insect on its host. The plants were then carefully dissected and examined for all the life stages of *T. texana*.

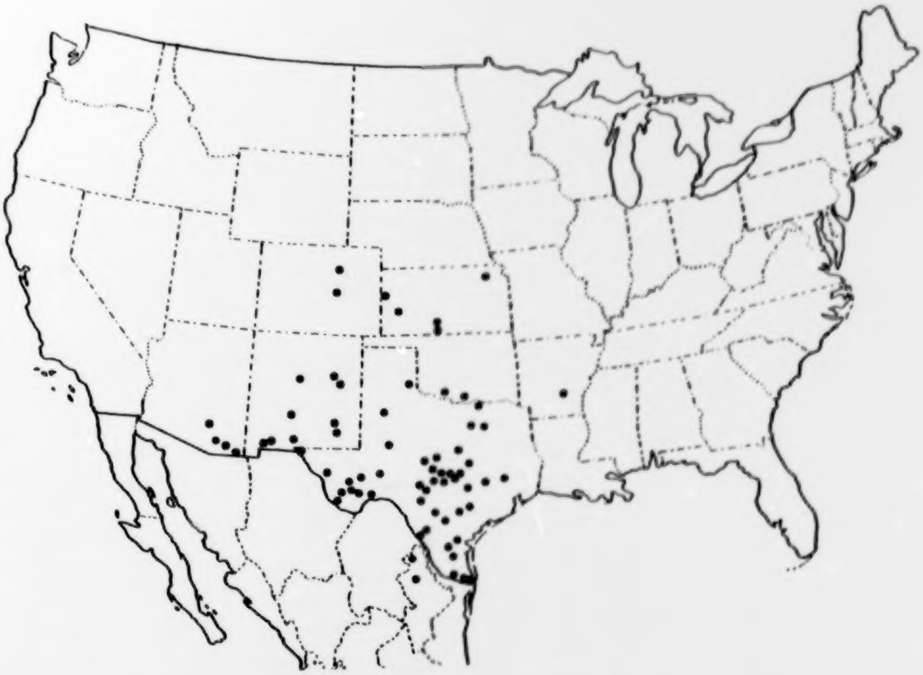

Fig. 2. Distribution of *Trichobaris texana* LeConte as determined by examination of specimens and from records in the literature.

All life stages recovered from the 1979 series of samples were counted and, except for parasitized individuals, preserved. Parasitized individuals were transferred to no. 3 gelatin capsules (1 host/capsule) to facilitate observations of subsequent parasite development. Hymenopterous parasites reared from the immature stages of *T. texana* were submitted to the Insect Identification and Beneficial Insect Introduction Institute, Beltsville, Maryland, for identification.

After identification and sexing, surviving adults of the 1978 generation were placed in feeding and oviposition cages (1 male, 1 female/cage). Each cage consisted of a plastic vial (*c.* 3 cm diam, 10 cm ht) furnished with a young terminal of SLN placed upright with the cut end in a *c.* 0.5 ml shell vial containing distilled water. Preliminary observations suggested that a young terminal with attached leaves was the most likely site of oviposition. A fresh terminal was provided daily from plants growing along roadsides. The plastic vial cage was closed with a foam rubber plug.

Eggs were dissected from the plant tissue and reared by following a method similar to that described by Goode and Randolph (1961) for laboratory rearing of the sugarcane rootstock weevil, *Anacentrinus deplanatus* Casey (Coleoptera: Curculionidae). Each egg was placed in a small depression made with forceps in the exposed pith of a *c.* 7 cm section of a SLN stem split longitudinally. The two plant sections were reassembled and sealed at each end with paraffin and then placed in a plastic vial cage (1 stem section/cage). The number and duration of the various stages of the insect were determined by breaking the paraffin seal, separating the two plant parts and observing the successive stages of development of the insect. Stem sections were reassembled and resealed with melted paraffin after each daily inspection and were replaced as needed.

The oviposition and rearing cages were kept on a laboratory bench in a rearing room at *c.* 24°C with fluorescent Grolux® lights on a 14L:10D photoperiod. Simple life and fertility tables were constructed for *T. texana* reared under constant temperature in the laboratory. Data for the construction of the life table were obtained from monitoring the fate of a cohort of eggs; data for the age-specific fertility table were obtained by monitoring oviposition and survival of previously unmated females exposed to males in the laboratory. The construction and interpretation of the life and fertility tables follow the methods summarized by Southwood (1978).

Voucher specimens of the developmental stages and parasites of *T. texana* were deposited in the Department of Entomology Insect Collection, Texas A & M University.

Results and Discussion

Biology of Trichobaris texana

The study of the biology of *T. texana* reported in this section includes laboratory and field investigations on all developmental stages.

Egg. Eggs of *T. texana* are yellowish, ovoid, *c.* 0.70 mm in length and 0.44 mm in width. All of the eggs deposited during this study were inserted in the petiole or midrib on the underside of a leaf near the base of the lamina.

The duration of the egg stage was 4–18 days and averaged 6.2 days (Table 1). Survival (% of larval eclosion) of the laboratory cohort of 108 eggs deposited by 10 females at *c.* 24°C was 88% (Table 2).

Eggs were observed in the field from mid-April to late June (Fig. 3); they were most numerous during the latter part of May. A maximum of 7 eggs was observed on a single plant, each deposited on a different leaf.

A mymarid, *Anaphes* sp. (Hymenoptera: Mymaridae), parasitized in excess of 10% of field-collected eggs (Table 3). This species is reported here for the first time as a true egg parasite of *T. texana*. Although the life cycle of this parasite was not studied, *Anaphes* sp. is a solitary, internal egg parasite, and its temporal distribution coincided with peak host density (Fig. 4).

Larva. Newly hatched larvae tunneled toward the base of the petioles, entering the stem pith as 2nd or 3rd instar larvae. Larval feeding inside the leaf petioles caused premature abscission of the leaves. Evidence for this early abscission was obtained by splitting the stems longitudinally to expose frass tunnels in the stem pith originating from leaf nodes.

Subsequent feeding and maturation of larvae occurred entirely within the stem pith of SLN. In a given plant, intraspecific competition between the developing larvae for food was generally fatal to all but a single larva. It was uncommon for 2 larvae to develop to maturity in the same plant as indicated by frequent observations of partially devoured or fragments of larvae mixed with frass. Although the exact nature and significance of this accidental cannibalism are unknown, one possible explanation for the observed intraspecific predation is increased survival of an individual at the expense of siblings (Eikwort 1973), assuming that a within-plant infestation of multiple larvae resulted from eggs produced and deposited by the same female.

Table 1. Duration (in days) of each immature stage of *Trichobaris texana* under laboratory conditions of *c.* 24°C and 14L:10D photoperiod.

Stage	No. completing stage	Range	$\bar{x} \pm$ SE	Cumulative mean age (days)
Egg	95[1]	4–18	6.20±0.22	6.20
Larva				
1st instar	70	1–10	4.13±0.23	10.33
2nd instar	53	3–11	5.23±0.20	15.56
3rd instar	42	4–10	5.52±0.18	21.08
4th instar	36	4–15	6.47±0.45	27.55
5th instar	27	5–13	6.67±0.29	34.22
6th instar	18	6–27	12.39±1.70	46.61
7th instar	5	7–21	15.60±2.31	62.21
Pupa	10	10–12	11.10±0.18	73.31

[1] 108 eggs were deposited.

Table 2. Life table for *Trichobaris texana* cohort reared at *c.* 24°C and 14L:10D photoperiod.[1]

x	l_x	d_x	L_x	T_x	e_x	$100q_x$	$100r_x$
Eggs	108	13	101.5	170.0	1.57	12.04	12.04
Larvae	95	84	53.0	68.5	0.72	88.42	77.78
Pupae	11	1	10.5	15.5	1.41	9.09	0.93
Adults	10	10	5.0	5.0	0.50	100.00	9.26

[1] e_x value represents life expectancy in 'life stages' remaining.

T. texana has 6 or 7 larval instars in the laboratory. The 1st, 2nd, 3rd, 4th, 5th, 6th, and 7th instars averaged 4.1, 5.2, 5.5, 6.5, 6.7, 12.4, and 15.6 days, respectively (Table 1). The duration of the entire larval period was 23–86 days for 6 instars and 30–107 days for 7 instars. Of the developmental stages of *T. texana*, the larval stage experienced the greatest mortality. Ten percent of the cohort survived the larval stage (Table 2).

The number of instars increases in many species of insects with insufficient or inadequate food (Gaines and Campbell 1935; Cuda and McPherson 1976; Frick and Wilson 1978); thus, the number of instars (6 or 7) observed for *T. texana* in the laboratory may have resulted from a dietary deficiency. To test the hypothesis of inadequate diet, head capsule measurements of preserved, field-collected larvae were analyzed by Dyar's 'Rule' (Dyar 1890) and the least squares method (Forbes 1934; Gaines and Campbell 1935; Cave and Smith 1983). Table 4 includes observed and expected values of head capsule widths for field-collected larvae of *T. texana*. The mean of the observed growth ratios ($r = 1.31$) was used as a common ratio for calculating an expected progression beginning with the first term of the observed progression. The observed and calculated values are reasonably close indicating Dyar's law corroborates the 6 or 7 instars observed in the laboratory.

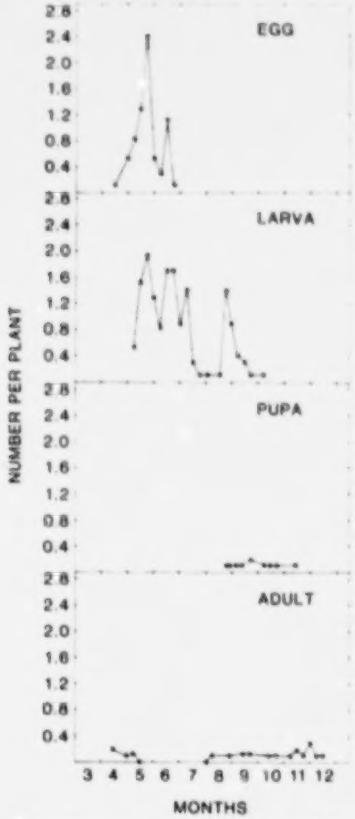

Fig. 3. Temporal distribution of the developmental stages of *Trichobaris texana* LeConte for 1979 on *Solanum elaeagnifolium* Cav. in Brazos County, Texas, U.S.A.

A perfect geometrical progression of head capsule widths can be represented by a straight line if the logarithms of the head measurements are plotted against the number of instars (Forbes 1934). A plot of the equation $\log Y = -0.687 + 0.119X$ for larvae of *T. texana* (Fig. 5) reveals a strong positive linear relationship between instar number and larval head capsule width ($r^2 = 0.985$). The expected values found by substituting for X in the foregoing equation are given in Table 4 together with the difference between them and the observed values. Although development was not perfectly geometrical, this linear model provides additional evidence that *T. texana* has 6 or 7 instars.

Larvae were found in field samples from the 2nd week of May to the 2nd week of October (Fig. 3). Parasites reared from the larvae were *Neocatolaccus tylodermae* (Ashmead) (Hymenoptera: Pteromalidae) and *Eurytoma* sp. (Hymenoptera: Eurytomidae) (Table 3). The latter could be *E. tylodermatis* Ashmead, which is known from existing host records to attack *T. texana* and *T. trinotata* (Burks 1979). In addition, a species of the genus *Eurytoma* was previously reported as a parasite of *T. texana* in stems of buffalobur, *S. rostratum* (Chesnut and Cross 1971); whether it is conspecific with the species attacking *T. texana* in SLN could not be determined. It should be noted that *N. tylodermae*, which accounted for 3.2% parasitism, was reared from larvae collected during preliminary sampling in 1978; it was not observed in 1979. Total larval mortality due to parasitism was 4.5%. The larval parasites were present from late July to early November (Fig. 4).

Table 3. Parasites of the egg and larval stages of *Trichobaris texana* on *Solanum elaeagnifolium*, 1978 and 1979, Brazos County, Texas, U.S.A.

Parasite	Host stage attacked	No. of each host stage collected	% Parasitism
Anaphes sp. (Hymenoptera: Myrmaridae)	Egg	104	10.6
Neocatolaccus tylodermae (Ashmead)[1] (Hymenoptera: Pteromalidae)	Larva	94	3.2
Eurytoma sp. (Hymenoptera: Eurytomidae)	Larva	237	0.8
Unidentified species [2]	Larva	237	Total 6.0

[1] Collected in 1978.

[2] Only host remains recovered.

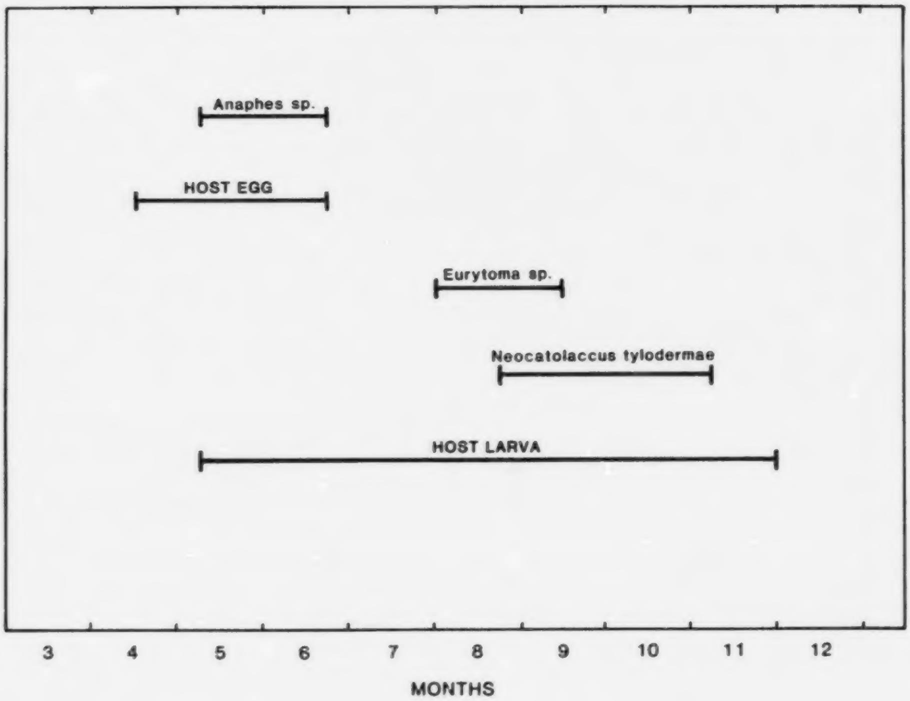

Fig. 4. Temporal distribution of the parasites of the egg and larval stages of *Trichobaris texana* LeConte during 1978–79, Brazos County, Texas, U.S.A.

Pupa. Mature larvae pupated in the stems of SLN. Prior to pupation, the larva bores a hole outward that penetrates the extensive woody secondary xylem but not the cortical or epidermal layers of the stem. This behavior facilitates subsequent adult emergence. The larva then constructs a pupal chamber of woody secondary xylem fibers before entering a nonfeeding quiescent prepupal period which in the laboratory lasted 4–9 days. The pupa is white to pale yellow initially but tanning of the pharate adult cuticle commences 9–11 days prior to eclosion. Under laboratory conditions, the pupal stage ranges from 10–12 days with an average duration of 11.1 days (Table 1). Nine percent of the laboratory cohort completed the pupal stage (Table 2).

Pupae were observed in field samples from late August to mid-November (Fig. 3). The appearance of new adults during the 2nd week of August (Fig. 3), however, clearly indicates pupae were present earlier but none were collected.

Table 4. Comparison of observed and expected values of head capsule widths (mm) of larvae of *Trichobaris texana*.

Instar	Observed[1]	Expected	Difference	% Difference
I	0.27	0.27[2]	0.00	0.00
		0.27[3]	0.00	0.00
II	0.38	0.35	+0.03	+8.57
		0.36	+0.02	+5.56
III	0.48	0.46	+0.02	+4.35
		0.48	0.00	0.00
IV	0.56	0.60	−0.04	−6.67
		0.62	−0.06	−9.67
V	0.73	0.79	−0.06	−7.59
		0.81	−0.04	−4.94
VI	1.14	1.03	+0.11	+10.68
		1.06	+0.08	+7.55
VII	1.40	1.35	+0.05	+3.70
		1.40	0.00	0.00

[1] Mode.

[2] Calculated from the mean of the observed Dyar ratios ($r = 1.31$) and the observed first term.

[3] Calculated by linear regression, using the equation $\log Y = -0.687 + 0.119X$.

Adult. Feeding, mating, and oviposition were observed in the laboratory. Adults feed on the epidermal layer and a few layers of underlying cells from small areas located on a leaf petiole or terminal portion of the stem.

A single pair was observed *in copulo* on three different dates. The adults assume the normal copulatory position with the male on the back of the female. Copulation was in progress each time this pair was observed but lasted an additional 115±54.1 min. for the three observations.

Oviposition commences 1–23 days after mating. One female was observed ovipositing. The female first chewed a hold deep enough to completely conceal the egg just below the epidermis of a leaf midrib. The excavation was placed ventrally near the base of the lamina. The female then turned 180°, located the hole with the tip of the abdomen, and inserted the ovipositor into the opening. After depositing the egg, the female returned to the original position and chewed two arcuate slits that united laterally forming an ellipse around the hole and, using these slits, excavated a chamber around the egg. The total time for oviposition and construction of the chamber was *c.* 30 min.

The reproductive capacity of *T. texana* was also measured in the laboratory. Three females were tested, each in a separate feeding and oviposition cage at *c.* 24°C and a 14 h photophase. Excluding the time spent in reproductive diapause (which is likely to be highly dependent on climatic conditions), active adult females lived a maximum of 39 days (avg. of 35±5.3 days). Peak oviposition occurred within *c.* 30 days after mating with a maximum production of *c.* 5 eggs/female/day (Fig. 6). The three females deposited from 10–44 eggs ($x \pm SD = 33 \pm 20$) each over a period of *c.* 5.5 wks.

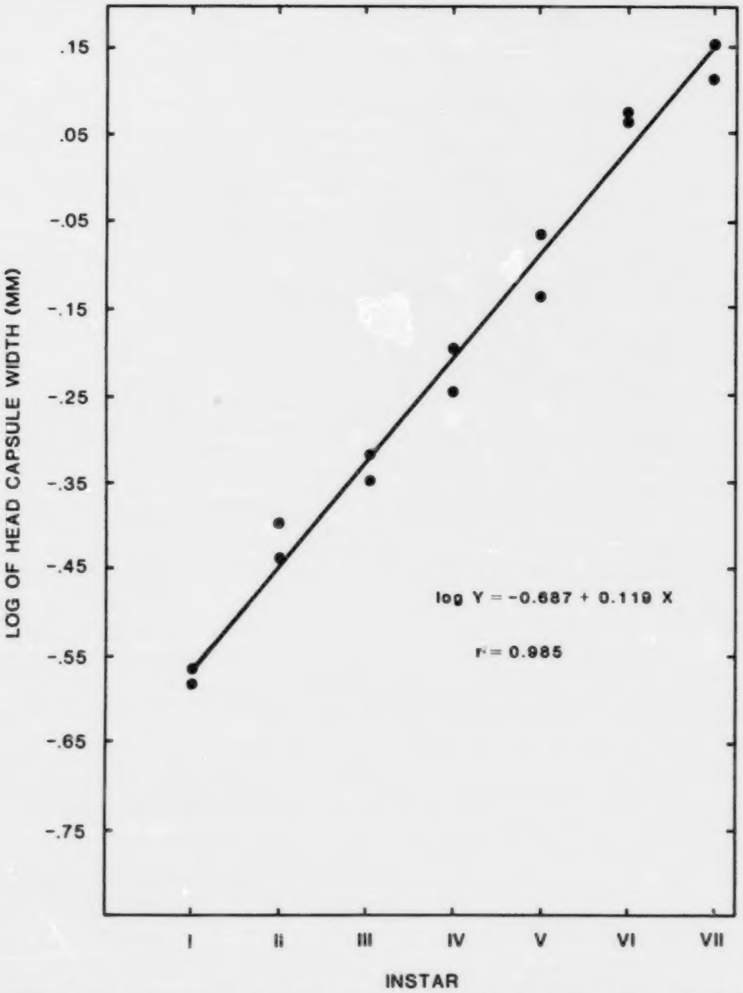

Fig. 5. Semilog plot of the mode larval head capsule widths of *Trichobaris texana* LeConte versus the number of instars using the regression equation, $\log Y = -0.687 + 0.119X$.

From laboratory rearing, duration and survival of the immature stages were found to be: egg — 6.2 days, 88.0%; larva — 56.0 days, 11.6%; and pupa — 11.1 days, 90.9%. Thus, the best estimate of total developmental time and survival through the immature stages was 74 days and 9.0%, respectively (Tables 1 and 2). When the number of living individuals within the cohort at a given age (l_x) were plotted against the age (x), the staircase type of survivorship curve with three distinct steps (Ito 1959) indicated that *T. texana* had three critical periods throughout its development — from the egg to the first larval instar, from the last larval instar to the pupa, and the senescent adult (Fig. 6).

Using the aforementioned information on duration and survival of the immature stages and that of oviposition and survival of the females, the basic population parameters were then calculated according to the methods of Birch (1948) and Laughlin (1965). The net reproductive rate (R_o) for *T. texana* was 1.41, the cohort generation time (T_c) was 92.55 days, and the capacity for increase (r_c) was 0.0037. Thus, the population would increase 1.004 times/day and 187 days would be required for the population to double.

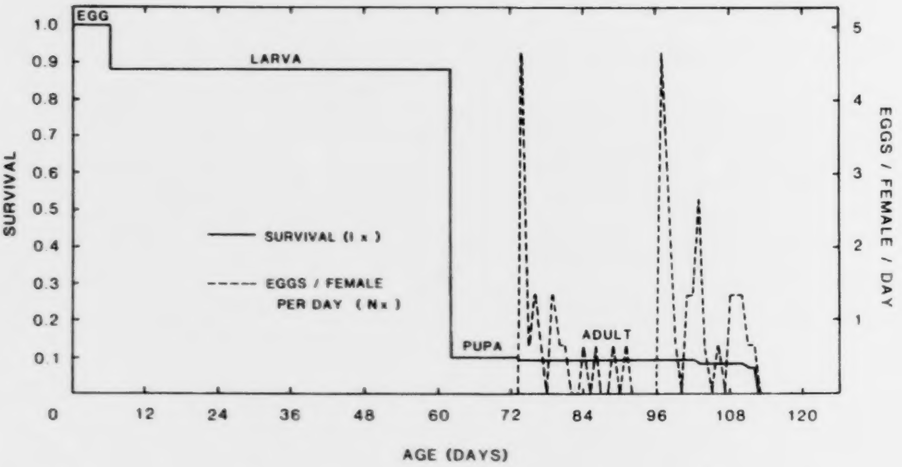

Fig. 6. Survival and age-specific oviposition of three newly emerged females of *Trichobaris texana* LeConte in the laboratory (survival of immature stages is based on a separate cohort of eggs).

In the field, adults emerged from overwintering sites and were present from mid-April to early May but died soon afterward (Fig. 3). Diapausing adults appeared inside the stems of SLN in early August; they were most numerous from mid- to late November (Fig. 3). In general, adults overwinter inside the stems but occasionally complete the excavation of the emergence hole initiated by the larvae, emerge from the stems, and apparently overwinter in adjacent ground litter. Although no adults were recovered from ground litter samples analyzed in December 1979 by the Berlese-Tullgren funnel extraction method (Southwood 1978), the ground litter hibernation site hypothesis is supported by the observation of adult emergence holes in stems of 6.0% of plants sampled between 3 October and 10 December and the report of an adult overwintering in old stalks of little bluestem, *Schizachyrium scoparium* (Michx.) Nash. (Poaceae) (Salsbury, pers. comm.).

Impact of Trichobaris texana *on Silverleaf Nightshade*

Since feeding of the larvae inside the stems is potentially destructive and will determine the efficacy of *T. texana* as a biological control agent of SLN, the effect of this feeding was evaluated by comparing the seasonal rate of growth (i.e. height) of normal and infested plants. After plotting the mean heights of infested and uninfested plants against time (Fig. 7), growth curves were fitted to the data by curvilinear regression. The asymptotic growth model of Snedecor and Cochran (1980), which is expressed by the equation:

$$Y = A - B(C^x)$$

where: Y = height (cm); x = time (days); A = maximum height; B = difference between maximum height and height at $t = 0$; and C = rate of growth, yielded significantly different estimates for A and B from infested and uninfested plants ($F_{3,62} = 20.633$, Table 5) when the reduced and full models were analyzed by the 'Extra Sum of Squares Principle' (Draper and Smith 1981). These data suggest that tunneling activity of larvae inside stems ultimately stunts growth of SLN.

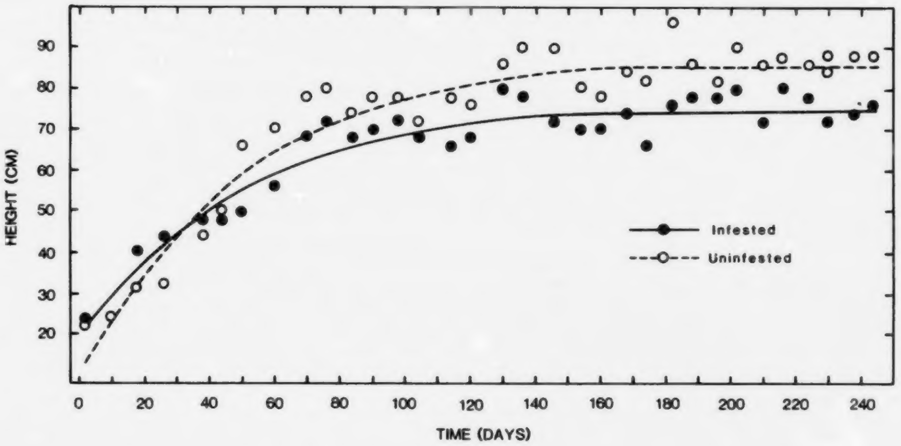

Fig. 7. Seasonal growth pattern of uninfested *Solanum elaeagnifolium* Cav. and plants infested with larvae of *Trichobaris texana* LeConte.

Table 5. Range of values of the coefficients of the asymptotic function fitted to the growth data on silverleaf nightshade at the 95% confidence interval.[1]

Coefficient	Uninfested	Infested
A	84.6 –91.1*[2]	72.8 –79.3*
B	69.1 –83.4*	47.8 –64.6*
C	0.976– 0.984	0.974– 0.986

[1] Model: $Y = A - B(C^x)$.

[2] Values across the row followed by an asterisk are significant at $P < 0.05$ according to the Extra Sum of Squares Principle (Draper and Smith 1981).

Conclusions

SLN is a major perennial weed in cultivated and otherwise disturbed areas both here and abroad. Millions of acres of cotton cropland in the southwestern United States are infested with this native weed (Orr *et al.* 1975). Furthermore, SLN was accidentally introduced into South Africa and Australia, where it also is becoming a troublesome weed in agricultural land and pastures (Siebert 1975).

Since chemical and mechanical control measures have met with limited success, biological control may be a viable alternative. To date, four species of insects and one nematode have been considered as candidates for biological control of SLN (Goeden and Ricker 1971; Siebert 1975; Julien 1982).

The results of this study suggest that *T. texana* may afford some measure of biological control for SLN. Infested plants are stunted by the stem-boring activity of the larvae. Since SLN reproduces both by seed and by perennial root propagation, the stem-boring action of this natural enemy may curtail regrowth from underground parts of the plant and thus reduce the rate of spread of this noxious weed.

The biology of *T. texana* was studied herein primarily to contribute to the limited knowledge of the Curculionidae. However, in view of this insect's apparent ability to retard the growth of SLN, continued research on the host range, climatic tolerances and potential control value of *T. texana* is recommended.

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Re-evaluation of the Biological Control Program for *Heliotropium europaeum* in Australia

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Abstract

Biological control in Australia of the summer-growing, Mediterranean annual weed common heliotrope, *Heliotropium europaeum*, is discussed. The order of introduction of biological control agents, based on European studies, was planned to be a root- and foliage-feeding flea beetle (*Longitarsus albineus*), followed by a crown- and foliage-feeding weevil (*Pachycerus madidus*), a bud-feeding moth (*Ethmia distgmatella*) and a rust fungus (*Uromyces heliotropii*). *L. albineus* was introduced into Australia in 1979, showed early signs of establishment, then died out due to consecutive, severe drought years. The program has been re-evaluated, based on a detailed study of the field ecology of the weed in Australia, which emphasized that plants must be affected early in summer, and seed production reduced, for biological control to be successful. The preferred order of introduction is now the rust, followed by the moth, the weevil and the flea beetle. Due to availability, ease of collection and the order in which host-specificity studies were conducted, however, it is likely that the weevil will be introduced next, followed by the rust, the moth and the flea beetle. Despite the order of introduction, integrated control, involving a suite of natural enemies of the weed, along with cultural treatments, is likely to be required to reduce and maintain this species below the economic threshold.

Réévaluation du Programme de Lutte Biologique Contre *Heliotropium europaeum* en Australie

Le rapport traite de la lutte biologique contre *Heliotropium europaeum* en Australie. D'après les études menées en Europe, les agents biologiques devaient être introduits dans l'ordre suivant: une altise (*Longitarsus albineus*), un charançon (*Pachycerus madidus*), un lépidoptère (*Ethmia distigmatella*) et un champignon provoquant la rouille (*Uromyces heliotropii*). *L. albineus* qui a été libéré en 1979, semblait d'abord bien s'établir, mais il a été décimé par la sécheresse. Le programme a de nouveau été évalué en fonction d'une étude approfondie menée sur le terrain sur les caractéristiques de cette plante nuisible en Australie; selon cette étude, il faut, pour que la lutte biologique soit efficace, que les plantes soient perturbées tôt en été et que leur production de graines soit réduire. L'on recommande actuellement d'introduire les agents dans l'ordre suivant: rouille, lépidoptère, charançon et altise. Toutefois, en raison d'autres facteurs qui font l'objet de l'étude, l'ordre d'introduction sera sans doute le suivant: charançon, rouille et lépidoptère. Le rapport traite de la lutte intégrée de *H. europaeum*.

Introduction

Common heliotrope, *Heliotropium europaeum* L. (Boraginaceae), is a summer-growing, annual, herbaceous plant originating in the Mediterranean and Middle East, which has become a major stock-poisoning weed in Australia. Distribution, biology, phenology, effects on livestock and control methods were reviewed by Delfosse and Cullen (1981).

Early surveys for natural enemies of the weed were conducted in 1950 in France, Spain, Algeria and Tunisia. It was concluded at that time that the weed was not a promising target for biological control. However, given the increasing importance of the weed to Australia, additional surveys were conducted in 1972 and 1974 in Iran, Tunisia and Algeria.

These surveys yielded 122 species from *Heliotropium* spp., including 2 fungi, 3 mites (plus unidentified species) and 117 insect species (2 Orthoptera, 1 Isoptera, 2 Thysanoptera, 33 Hemiptera, 13 Homoptera, 49 Coleoptera, 11 Lepidoptera, 4 Diptera and 2 Hymenoptera) (Delfosse and Cullen 1981). Of these, six species are currently being considered for biological control of *H. europaeum* in Australia: *Longitarsus albineus* (Foudras) (Coleoptera: Chrysomelidae), *Pachycerus madidus* (Ol.) (= *P. cordiger* Germ.) (Coleoptera: Curculionidae), *Ethmia distigmatella* Erschoff (Lepidoptera: Ethmiidae), *Uromyces heliotropii* Sredinski (Uredinales), *Cercospora* sp. (possibly *C. heliotropii-bocconi*) (Hyphomycetes), and *Utethesia pulchella* (L.) (Lepidoptera: Arctiidae). Other species, at this time considered to be of minor importance (Wapshere 1982), may be considered for introduction later.

In this paper the previously determined order of introduction of biological control agents for *H. europaeum* is re-examined using new information on the ecology of the weed, results of releases of *L. albineus*, and examination of the available information on the biology of the agents in reference to their host. I then recommend a new order of introduction of *H. europaeum* agents, and discuss the reasons why this may be difficult to follow.

Original Preferred Order of Introduction

Wapshere (1982) rated the six main species in the following order: *L. albineus*, *P. madidus*, *E. distigmatella*, *U. heliotropii*, *Cercospora* sp. and *U. pulchella*. These ratings were based on detailed studies of the ecology of *H. europaeum* in Mediterranean Europe to north Africa, including effects of the natural enemies of the weed there, studies on the agents themselves, and ease in obtaining the species for host-specificity studies.

Biology of the Main Species

L. albineus, *the Heliotrope Flea Beetle*

This is the most-studied of the six main species: biology, host-specificity, and rearing techniques have been investigated in Europe (Huber 1979, 1981). Adults feed on foliage; larvae feed on rootlets and cause most stress to their hosts (Fig. 1). In spring, overwintering adults feed on *Heliotropium* foliage, mate, and lay eggs in soil crevices at the bases of *Heliotropium* spp. soon after germination. Larvae feed externally (rarely internally) on rootlets. Two to three larvae can kill a seedling. Larvae pupate in the soil near their host plants, generally within 10 cm of the soil surface. Three generations occur each summer, with the third generation adults being the overwintering (diapausing) stage. Generations overlap in summer.

Adult overwintering survival is low (2.4% of caged adults), and egg–adult survival is 54.1% (Huber 1981). Overwintering females mated once laid a mean of 270.7 eggs/female; summer females lay a mean of 261 eggs. Ovipositing females create a mean of 15.1 shot holes/day in heliotrope leaves; males, 6.0/day. Shot holes average 1 mm diam. The sex ratio of all generations is *c.* 1:1. Flower petals are also sometimes shot-holed.

A heavy infestation of adults in Cap d'Age, France, produced a mean of 123.6 shot holes/leaf by August, in a plot with a density of 10–200 *H. europaeum* plants/m^2 (Huber 1981). Despite this level of stress, no significant decrease in plants/m^2 was noted; most plants were < 20 cm high, but all produced seed. At Bessan (Hérault) France, heavy attack by *L. albineus* killed or stunted plants (Huber 1981).

There are two periods/year when adults disperse widely: late autumn, when they seek cover after death of *H. europaeum*; and early spring, before germination of *H. europaeum*.

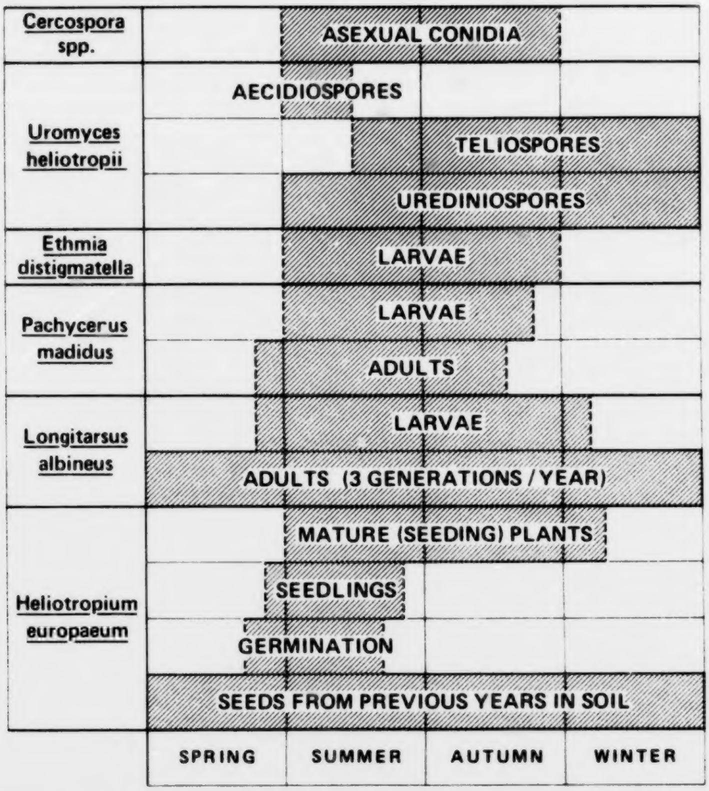

Fig. 1. Summary of stages of biological control agents which stress common heliotrope, *Heliotropium europaeum* L., in relation to the important stages of the weed to be attacked if biological control is to be successful. (Vertical dashes at ends of bars indicate that occurrence of stages can vary in time from year to year.)

P. madidus, *the Heliotrope Weevil*

Huber, Vayssiéres and Wapshere (pers. comm., 1984) investigated the biology and host-specificity of this univoltine species. Adults emerge from soil shortly after germination of *H. europeaum* in spring. They disperse rapidly, searching for their host. Adults cut large holes in leaves. Eggs are attached to the stem of plants near ground level, and are covered with a faecal glue. Larvae descend to the root crown, where they construct an earthen cell, and feed on the root. Pupation occurs in an earthen cell close to the root, and lasts *c.* 2 wks. Adults overwinter in the earthen cell until the following spring.

No specific information is yet available on the fecundity, longevity or dispersal of *P. madidus* in Europe.

Adults are voracious feeders. During their *c.* 8-wk period of activity, they can strip *Heliotropium* spp. of their leaves and kill seedlings by cutting stems. Larvae can kill thinner-rooted plants, and adults can weaken larger plants by cutting holes in leaves (Fig. 1).

Ethmia distigmatella, *the Heliotrope Flower-Feeder*

Larvae of this species are the only flower-feeders known from annual *Heliotropium* spp. in the Eastern Mediterranean Europe and Middle East (Wapshere 1982) (Fig. 1). Host-specificity testing has not been conducted, but some observations on the specificity and biology of this species have been made.

One factor in particular indicates that this species is likely to be restricted to a small group of Boraginaceae related to *Heliotropium* (A.J. Wapshere, pers. comm., 1984): larvae are dependent on a linear, compact floral cyme for completion of development. Therefore, plants not having such floral anatomy are probably not at risk from larval attack. *Ethmia* spp. have usually been recorded from Boraginaceae, although a few develop on plants in the related family Hydrophyllaceae (Sattler 1967; Powell 1973, 1980).

Uromyces heliotropii, *the Heliotrope Rust*

This rust fungus has been found only four times (Wapshere 1982), despite examination of many sites from Mediterranean Europe to north Africa since 1971 (Delfosse and Cullen 1981). It is autoecious and macrocyclic, and host-specificity studies are underway (Hasan and Cullen 1984*a*, *b*; Hasan 1985). Preliminary testing indicates that it is restricted to a small, closely related group of *Heliotropium* spp. (S. Hasan, pers. comm., 1984).

The life cycle of this species is complicated (S. Hasan, pers. comm., 1984; Hasan and Cullen 1984*a*). Aecidia appear in late winter–spring, and aecidiospores infect seedlings upon germination. Uredinia are then developed, giving rise to urediniospores, which in severe attacks, cover the entire plant. Several generations of urediniospores occur through summer, and this is the main multiplicative and dispersal stage in the life cycle (Fig. 1). During late summer–autumn, telia and teliospores are produced on mature plants. Some teliospores infect plants immediately; others overwinter, along with uredinia and aecidia, on dead leaves. Aecidiospores germinate on seedlings the following spring, forming spermagonia, aecidia and aecidiospores. Aecidiospores then give rise to urediniospores. In Turkey, the limiting factor is lack of suitable host plants (S. Hasan, pers. comm., 1984).

Cercospora *spp.*

These leaf blotch fungi cause partial defoliation of *Heliotropium* spp. (Fig. 1), but as they are the asexual stage of imperfect fungi whose sexual stage is often not known, and have an unknown host range, there could be difficulties in determining host-specificity and quarantine safety (Wapshere 1982). They can be cultured on artificial medium, and causes brown, circular to sub-circular lesions on leaves (Hasan and Cullen 1984*b*).

However, I collected *C. taurica* Tranzsch., a European species, from *H. europaeum* in northern N.S.W. in 1982. Only two other collections of this species have been made in Australia, both from *H. europaeum* in N.S.W., one each in 1943 and 1953 (J. Walker, pers. comm., 1984). Thus, in > 40 years in Australia, there have been no records of attack by *C. taurica* on other species, and it appears that the fungus has not spread widely. Location of a more virulent strain of *C. taurica* to *H. europaeum* may result in heavier attack on the weed in Australia.

Utethesia *spp., the Heliotrope Moths*

Larvae of *U. pulchella* (the European heliotrope moth), defoliate *Heliotropium* spp. in late summer (Wapshere 1982) (Fig. 1). By this time plants have dropped significant amounts of seed, and it is doubtful if there are any control benefits from these attacks. A related species, *U. pulchelloides* (L.) native to Australia, also attacks *H. europaeum* in a similar way and time. Unless large numbers of larvae can be released soon after germination in late spring (which is being investigated in Australia for *U. pulchelloides*) (Delfosse, unpubl. data), these species will be of little benefit in management of the weed. Therefore, they rank lowest of all presently known common heliotrope biological control agents.

Releases of *L. albineus* and Ecology of the Weed in Australia

L. albineus was first released in Australia in December 1979 (Delfosse and Cullen 1981). Other releases were made in 1981 (Delfosse and Cullen 1982; Delfosse, unpubl. data). Adults were recovered from all three release sites 1–2 yrs after release, but in very low numbers — despite seemingly good conditions for establishment. A severe drought occurred in Australia in 1980–83. At one release site, virtually no *H. europaeum* germinated; at the other two sites, there was very little germination compared to a normal year. No recoveries of *L. albineus* have been made since the drought broke in 1983, and establishment does not appear to have occurred.

The ecology of *H. europaeum* in Australia has been investigated by Moore (1956) and others (summarized in Delfosse and Cullen 1981). Five additional years of studying the ecology of the weed in the field in Australia, with emphasis on those factors likely to influence biological control, allow the following generalizations to be made. As in Europe (Huber 1981), *H. europaeum* in Australia rarely appears in large numbers at the same site two years in a row unless cultivation or heavy grazing occurs which buries or removes litter. The plants germinate in spring–early summer, when a combination of increasing soil temperatures and adequate rainfall occurs. If rainfall occurs only in late summer–early autumn, few plants germinate. Plants begin to set seed in the field as young as 2–3 wks and as short as 1 cm. Seeding continues until frosts kill plants in autumn–winter. Heavy grazing by sheep will reduce plant size, but in heavy infestations, will not prevent some plants seeding.

Discussion and Revised Order of Preferred Introduction

Successful biological control agents for *H. europaeum* should be capable of attacking plant growth early in the season, causing a significant decrease in seed set (Delfosse and Cullen 1981). Decrease in size of individual plants is also considered to be important, but will not contribute to control of the weed unless seed set is also reduced.

In theory two things are needed: (1) the current season's plants must be prevented from seeding significantly — if this happens, the already-large soil seed load (up to 30,000/m^2, Delfosse, unpubl. data) will not increase significantly; and (2) in subsequent years, biological control agents must be active early in the season, so that seedlings are prevented from seeding significantly. In this way, the soil seed load will be depleted over several years, and the weed can be managed.

How do the known biological control agents for *H. europaeum* fit into this scheme?

The main period of activity of *L. albineus, P. madidus* and *E. distigmatella* is during the hottest and driest time of the year in Mediterranean Europe (Wapshere and Cullen 1984). All three are dormant from autumn to late spring.

The poor field performance of *L. albineus* after release in Australia, its characteristics of high winter mortality and wide dispersal in autumn and spring, and the lack of damaging adult and larvae populations in the critical early season period when the plants are most susceptible to being stressed or killed (Fig. 1), and the difficulty of rearing large numbers in the laboratory, all mitigate against giving this species high priority for re-introduction. Indeed, its greatest effect on *H. europaeum*, unless a very large overwintering cohort of adults could be attained, only occurs after first generation adults emerge and lay eggs. By this time, a great deal of seeding has already occurred.

P. madidus must be rated as a better candidate than *L. albineus*, because adults are protected in earthen cells during winter and adult mortality over winter and dispersal are likely to be lower. Larger numbers of adults should thus be active earlier in the *H. europeaum* season. Also, it is very damaging to *H. europaeum*. However, since its period of greatest activity is also from mid-season onward, it is not the preferred species for introduction.

E. distigmatella appears to become active early in the season. Other *Ethmia* spp. lay up to *c.* 125 eggs/female (Powell 1981); if *E. distigmatella* proves to be in the high end of the scale of fecundity of this group of moths, it could have a major effect on reducing seeding of young plants at the time of year when stress is needed most.

Despite severe damage by larvae, *U. pulchella* become active too late in the heliotrope season to rank highly as a candidate for introduction, and its host range is unknown (although likely to be restricted to a small group of Boraginaceae) (Wapshere 1982).

Cercospora spp. occur mainly in the wetter areas of the Mediterranean coast of north Africa (Wapshere 1982). Thus, despite being active very early in the season, they may not be adapted to semi-desertic areas of Australia where *H. europaeum* is a problem.

U. heliotropii has all spore stages occurring on heliotrope, three of which are active early in the season. Urediniospores in particular can inflict extremely high mortality on early seedlings and mature plants.

Considering the positive and negative aspects of all known potential biological control agents for *H. europaeum*, plus the requirement to reduce significantly or eliminate seeding of the plant to effect long-term control, the preferred order of introduction of agents is: *U. heliotropii, E. distigmatella, P. madidus, L. albineus, U. pulchella,* and (pending more information on biology, ecology, epidemiology and host-specificity), *Cercospora* spp.

However, there are practical difficulties to implementing this scheme. Host-specificity testing is complete only for *L. albineus*. It is also the most common and widespread species on *Heliotropium* spp. in Mediterranean Europe to north Africa, but very difficult to mass-rear in the laboratory. Host-specificity testing for *P. madidus* was apparently completed in 1981 using the criteria established for *Dialectica scalariella* (Zeller) (Lepidoptera: Gracillariidae), a biological control agent for *Echium plantagineum* L. (Boraginaceae) (Wapshere and Kirk 1977). Application to Australian quarantine authorities for an introduction/release permit was made in late 1981, but testing of three genera of native Boraginaceous plants was then additionally required. Despite reasoning on ecological grounds against this additional, unplanned testing, it was required. Two of the three genera are difficult to find in the field, and have never been cultivated. Two years were spent in Australia collecting and developing cultivation techniques for these species, and further field trips to Greece were necessary to collect new adults for testing. Testing for *P. madidus* is expected to be completed by late 1985, with release in Australia (if safety is established) to occur soon after. It is likely that *P. madidus* will feed, but not be able to complete development, on these additional species. Thus, there could be a conflict of interest between graziers and conservationists. This may require quarantine authorities to arbitrate between the release of an exotic organism for possible control of a weed that can cause many million dollars damage when present in large amounts, and possible, slight damage to minor, sometimes rare, non-economic plants that generally do not occur in the range (or habitat) of the weed.

An approved list of test plants for *E. distigmatella* is being prepared, and testing should begin in 1985 (Cullen, pers. comm., 1984).

Host-specificity testing for *U. heliotropii* is not expected to be completed before early 1985, perhaps too late to obtain an importation/release permit in time to mass-culture the species for field releases during the 1984–85 season.

Host-specificity testing for *U. pulchella* and *Cercospora* spp. have not yet begun.

Whatever the eventual order of introduction, it is likely that a complex of organisms attacking all plant parts, will be required for long-term management of *H. europaeum*. It will be necessary to develop integrated control practices, using the biological control agents and cultural control methods. The first priority, however, must be given to species which attack recently germinated plants (*U. heliotropii*) and developing seeds (*E. distigmatella*).

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Effect of the Gall Midge, *Zeuxidiplosis giardi* (Diptera: Cecidomyiidae), on Seedlings of St. John's Wort, *Hypericum perforatum* (Clusiaceae)

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Abstract

A chemical exclusion trial was done in the field to determine the effect of the gall midge, *Zeuxidiplosis giardi*, on 200 paired St. John's wort seedlings. One member of each pair was protected against attack from the gall midge by regular, alternate applications of fenthion and monocrotophos. By the end of the trial the growth rate of the sprayed seedlings was almost four times that of the unsprayed seedlings. Survival of the unsprayed seedlings was 15% lower than that for the sprayed seedlings. *Z. giardi* therefore suppressed growth and reduced survival of St. John's wort seedlings in the field.

Effets du Moucheron Provoquant la Gale (*Zeuxidiplosis giardi*) (Diptère: Cecidomyiidae) sur les Jeunes Plantes de *Hypericum perforatum* (Clusiaceae) en Afrique du Sud

Le taux de survie, la croissance et le développement des jeunes plantes de *Hypericum perforatum* ont fait l'objet d'une surveillance pendant une période de 70 semaines afin de déterminer les effets des gales provoquées par *Zeuxidiplosis giardi*. Un membre de chaque 200 paires de jeunes plants combinés a été protégé contre la gale par des applications régulières d'insecticide. Quarante pour cent des plantes protégées et 25% des plants non vaporisées ont survécu. À la fin de l'essai, le taux quotidien de croissance de nouvelles feuilles était presque quatre fois plus élevé sur les plantes protégées (en l'absence de gale) et la masse moyenne finale en poids sec des jeunes plants vaporisés était environ deux fois plus élevée que celle des jeunes plants non protégés qui ont survécu. Seules huit inflorescences ont été produites par les 49 plantes non vaporisées qui ont survécu tandis que 43 inflorescences ont été relevées parmi les 79 jeunes plants vaporisés qui ont survécu. Les conclusions établissent donc que l'insecte réduit de façon marquée le taux de survie, de croissance et de floraison de *Hypericum perforatum*.

Introduction

St. John's wort, *Hypericum perforatum* L. (Clusiaceae), is an herbaceous perennial of Eurasian origin that has become an important weed in different parts of the world (Goeden 1978). It was first found in South Africa in 1942, and despite subsequent attempts to eradicate it chemically, it still occurs in localized patches in the South-Western Cape Province of South Africa (Gordon 1978).

Biological control of St. John's wort was initiated in South Africa with the introduction of *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) between 1960 and 1962 (Annecke and Neser 1977); this beetle has since successfully controlled St. John's wort growing in dense stands. The gall midge, *Zeuxidiplosis giardi* Kieffer (Diptera: Cecidomyiidae), was introduced in 1972 to supplement *C. quadrigemina* (Annecke and Neser 1977). *Z. giardi* has not been particularly successful in biological control programs in other parts of the world (Andres *et al.* 1973; Huffaker *in* Given

1967), except in Hawaii where it was thought to have contributed to the control of St. John's wort (Davis and Chong 1968).

Many workers have speculated about the effect of galling by *Z. giardi* larvae on St. John's wort (Wilson 1943; Holloway and Huffaker 1953; Given 1967; Currie and Garthside 1932), but none of the possible effects, which include suppressed growth of the plants, reduced competitive ability, increased mortality and reduced seeding, have ever been evaluated experimentally.

In this study, the effects of the gall midge on growth and survival of St. John's wort seedlings in the field were quantitatively determined. From observations in the field, it appeared that *Z. giardi* attack was most destructive on this stage.

Materials and Methods

Experimental Site

The trial was set up in disturbed vegetation on a southeast facing slope above Ida's Valley dam near Stellenbosch (33°54′S, 18°54′E). This site is in a winter rainfall area that has a mean annual rainfall of 990 mm. Rainfall and temperature data (Fig. 1C) collected during the trial were recorded at a weather station in Stellenbosch, about 4 km away.

Two hundred St. John's wort seedling pairs, each with 2–6 leaf pairs, were selected over a distance of 150 m and matched with regard to their size and situation. The positions of each of these seedlings was marked with a metal stake. From the number of galls on plants in the vicinity, it was evident that *Z. giardi* was abundant at the experimental site. During the course of the trial, midge activity was monitored by making regular counts of galls that appeared to contain larvae or pupae on marked seedlings. Any other damage on above-ground parts of the plants was also noted.

Exclusion of Z. giardi *by Insecticides*

One seedling in each pair was randomly assigned to be sprayed to run-off with the insecticides fenthion (*O-O*-dimethyl *O*-[3-methyl-4-(methylthio) phenyl] phosphorothioate; Lebaycid® emulsifiable concentrate at 0.5 mg AI/litre) and monocrotophos (*O-O*-dimethyl-*O*-(2-methylcarbamoyl-1-methyl-vinyl)-phosphate; Azodrin® emulsifiable concentrate at 0.4 mg AI/litre). Fenthion was included because it has both a contact and a systemic effect. Except for the effect of monocrotophos on sorghum, neither of these two insecticides are considered widely phytotoxic at the given dosages (Thomson 1982). The chemicals were sprayed alternatively at approximately 10-day intervals (depending on the weather) with a hand atomizer. The control seedlings were sprayed in the same way with comparable amounts of distilled water. Precautions were taken to avoid spray drift.

Measurement of Seedling Growth and Survival

Plant growth was monitored by counting the number of leaf pairs along the stems. Twelve counts were made at 4–7-wk intervals between 18 September 1979 and 20 January 1981 (70 wks). Growth rates of sprayed and unsprayed plants were then compared by means of a straight line estimate of the growth rate (Fig. 1B) using the formula (Pianka 1974):

$$\text{Growth rate} = \frac{N_{t1} - N_{t0}}{t_1 - t_0}$$

where N_{t0} = number of leaf pairs at the start of a period of time (t_0), and N_{t1} = number of leaf pairs after a period of time (t).

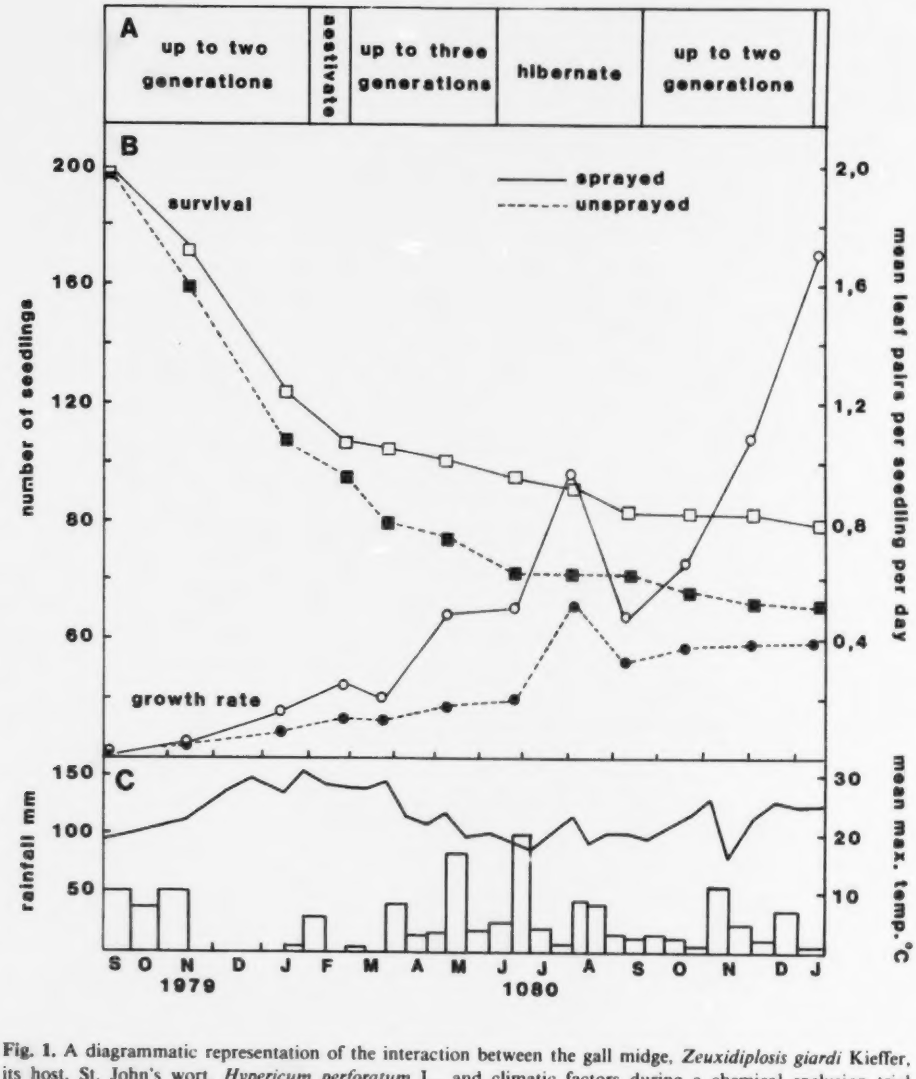

Fig. 1. A diagrammatic representation of the interaction between the gall midge, *Zeuxidiplosis giardi* Kieffer, its host, St. John's wort, *Hypericum perforatum* L., and climatic factors during a chemical exclusion trial showing: (A) the seasonal activity of the gall midge; (B) the survival and growth rate of the sprayed and unsprayed St. John's wort seedlings; and (C) the temperature and rainfall over this period.

Overall growth of the two groups was compared by determining the dry mass of the surviving plants at the end of the trial. After these plants had been carefully lifted, and the soil had been washed from their roots, they were placed separately in paper bags, dried in an oven at 20°C for 36 h and weighed. The number of upright flowering stems on each plant was also noted. Survival was followed by recording the mortality of plants at each count.

Results and Discussion

Effects of Z. giardi *on Growth*

The growth rate of unsprayed plants, that were subject to *Z. giardi* attack, was always less than that of sprayed plants (Fig. 1B). The cumulative effect of *Z. giardi* on the growth rate is shown towards the end of the trial where, while the growth rate of sprayed seedlings increased markedly from 0.47 leaf pairs/seedling/day in September 1980 to 1.75 leaf pairs/seedling/day in January 1981, the growth rate of unsprayed seedlings remained below 0.38 leaf pairs/seedling/day over the corresponding period. The marked increase in the growth rate of all seedlings during July may be due to increasing temperatures over this period (Fig. 1C). Unsprayed seedlings reached their maximum growth rate during the same period which coincided with hibernation of the gall midge larvae (Fig. 1B).

Table 1. Comparison of the dry mass of the seedlings of St. John's wort, *Hypericum perforatum* L., at the end of the chemical exclusion trial.[1]

		Dry Mass (g)		
Treatment	*n*	*x*	range	s
Sprayed	76	1.69 *a*	0.01-14.99	2.96
Unsprayed	46	0.59 *b*	0.01- 5.89	1.06
Galled	38	0.60 *b*	0.01- 5.89	1.06
Ungalled	8	0.56 *b*	0.01- 3.10	1.09

[1] *a,b* = Different consonants denote significant differences at P = 0.05.

The mean dry mass of surviving unsprayed plants was only 34.9% of the mean dry mass of surviving sprayed plants ($P = 0.01$) (Table 1). Although *Z. giardi* activity was recorded during the whole trial, not all unsprayed seedlings were galled at any one time. This raises the question as to whether unsprayed seedlings were in fact all attacked by *Z. giardi*. The mean dry weight of the eight surviving unsprayed, ungalled seedlings was 0.56 g compared with 0.59 g of the unsprayed group as a whole (Table 1). The growth of the former was therefore apparently suppressed despite the absence of galling. It can be assumed that these relatively small, almost stunted seedlings were also attacked by *Z. giardi*, but that the young larvae failed to induce cecidogenesis, very likely because these particular plants were generally stressed by the adverse conditions, and because galls only develop in actively growing shoot tips and buds.

The midge prevented normal development of upright flowering stems. A total of eight uprights were produced by the surviving 49 unsprayed plants, compared with 43 uprights on 79 sprayed plants. In the latter instance up to four uprights were counted on a single plant. By suppressing growth of seedlings, *Z. giardi* prevented flowering in the first year and delayed maturation of the plant.

Effects of Z. giardi on Survival

Seedling mortality in both groups was high; this is a common phenomenon in St. John's wort seedlings (Clark and Clark 1952; Clark 1953; Smith 1958). The pattern of survival in both groups was similar with approximately 80% of mortality occurring within the first 190 days (Fig. 1B). This initial mortality coincided with the hot, dry summer (22.8% of total rainfall measured during the course of the trial fell over this period). With the onset of winter rains and drop in temperatures, seedling mortality levelled off. This trend agrees with the findings of Clark and Clark (1951), Clark (1953) and Smith (1958), who concluded that temperature and rainfall (especially distribution of rainfall) are the most important causes of seedling mortality in St. John's wort populations.

The survival of unsprayed seedlings was, however, still reduced by 15% compared to that of sprayed seedlings. In view of the importance of climate, it is concluded that *Z. giardi* only contributed to mortality by modifying the shape of the survivorship curve. The shape of the curve was primarily determined by climatic factors. The effect of the midge on young seedlings was accentuated by the dry summer following their establishment.

No noteworthy feeding damage of the beetle *C. quadrigemina* or any other organism was recorded.

This study has shown that *Z. giardi* reduces overall growth of St. John's wort seedlings, thereby reducing seedling survival. While this trial demonstrates the effect of *Z. giardi* on seedlings, another study that includes plants of all age groups within the population would be required to determine the overall value of *Z. giardi* as a biological control agent for St. John's wort. The fact that the growth rate of unsprayed seedlings was consistently reduced towards the end of the trial (Fig. 1B) suggests that *Z. giardi* is able to influence the growth rate of older plants. Nevertheless, *Z. giardi* is probably helping to increase the effectiveness of the other biological control agent, *C. quadrigemina*, by delaying recovery of St. John's wort after periodic population crashes which are caused by *C. quadrigemina* (Clark 1953).

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Suppression of Reproduction of Woody Weeds Using Insects which Destroy Flowers or Seeds

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Abstract

The use of insects for suppressing the reproduction of woody weeds is reviewed for 11 biological control programs. Although the level of flower and seed predation due to introduced insects has been estimated in some programs, quantitative data on the effects of introductions are unavailable. The potential of flower- and seed-feeding insects for controlling the growth and spread of woody weed populations is discussed and situations where seed destruction may affect control of a weed are identified.

Contrôle de la Reproduction et de l'Extension des Plantes Nuisibles Ligneuses par le Moyen des Graines

Le rapport traite de l'utilisation des insectes pour enrayer la reproduction et l'extension des plantes nuisibles ligneuses par le moyen de graines dans le cadre de 11 programmes de lutte biologique. Bien que le degré de destruction des graines avant leur dispersion provoquée par l'introduction d'insectes ait été évalué dans le cadre de certains programmes, il n'existe aucune donnée quantitative sur les effets de cette méthode de contrôle. L'auter fait état de l'efficacité probable des insectes granivores pour lutter contre les infestations des plantes nuisibles ligneuses et indiquer les situations où la destruction des graines peut influer sur la lutte contre une plante nuisible.

Introduction

The possession of long-lived seed banks, prolonged or repeated reproduction, development of mixed age-structure populations and immigration of seeds from other habitats, mean that the persistence of many populations is not critically dependent upon current seed populations (Cohen 1968; Hill 1977). However, production and survival of seed may be considerably reduced by insects (Singh and van Emden 1979; Louda 1982). This paper discusses suppression of reproduction of woody weeds using insects which destroy flowers or seeds and how reduction in seeding may influence the status of introduced species.

Insects may reduce seeding by stimulating galling of flower buds or flowers (e.g. eriophyiid mites, gall wasps, gall flies — usually no flowers are formed following attack), destroying flower buds or flowers prior to seed set (e.g. Lepidoptera, bugs, weevils) or destroying immature or mature seeds (e.g. Lepidoptera, bruchids, weevils). Insects from all these groups have been used in biological control programs.

Insects Affecting Seeding

Insects which attack flowers or seeds have been used in biological control programs directed at over 20 woody and herbaceous weeds (Goeden 1978; Julien 1982). In the

11 programs directed at woody weeds, 19 species of insects from 10 families have been used. The family Bruchidae has been used against four species, the Curculionidae against three, three other families each against two and the other families each against one. The target weeds are from seven families, six each being represented by one species and one, the Leguminosae, by five species (Table 1).

In the following programs, post-liberation studies were lacking or comprised simple estimates of the amount of seed destroyed. No attempt was made to correlate seed destruction with any change in the reproductive potential of the weed, its population density or its rate of spread.

In 1949–50, *Eurytoma attiva* Burks (Hymenoptera: Eurytomidae) was introduced into Mauritius to reduce seeding by *Cordia macrostachya* (Jacquin) Roemer & Schultes (Boraginaceae). This wasp established quickly and by 1951 16–81% (avg. 53.7%) of seeds were infested. In February, June and October 1953, infestations averaged 64.7, 40.8 and 48.7%, respectively. In summer, when seed production was at its maximum, infestation was 70–80% (Williams 1960). The same insect was introduced into Malaysia in 1977. By 1979 it had spread throughout the country and levels of infestation from 33.3–82% were recorded (Ung and Yunus 1981). The role of *E. attiva* in controlling *C. macrostachya* has not been assessed in either country, but Williams (1960) suggested that in Mauritius, *E. attiva* activity, combined with that of a leaf-feeding insect, *Metrogaleruca obscura* (DeGeer) (formerly *Schematiza cordiae* Barber; Coleoptera: Chrysomelidae), resulted in more stable control than would have been achieved by either insect.

Exapion ulicis (Forster) (Coleoptera: Curculionidae), was established in New Zealand in 1931, Australia in 1939, U.S.A. in 1953 and Hawaii in 1955–56 to reduce the seeding and spread of gorse, *Ulex europaeus* L. (Leguminosae). Estimates of seed destruction are variable, with figures of 20 to > 90% for New Zealand and, in areas of the U.S.A., 'almost every gorse pod contained 3–10 beetles' (Goeden 1978, p. 396). Whereas the introduction of *E. ulicis* was regarded as having partially achieved its objectives in New Zealand and the U.S.A., it has not reduced the rate of spread of gorse in Australia or Hawaii (Goeden 1978; Julien 1982).

In 1968, Harley (unpubl. data) applied insecticides to protect plants of three taxa of *Lantana camara* L. (Verbenaceae) from attack by the biological control agents, *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae), *Ophiomyia lantanae* (Froggatt) (Diptera: Agromyzidae) and several other control agents of lesser importance. The production of seed-bearing receptacles in these plants increased from 0 up to 54 over three months, whereas those plants not protected by insecticide produced no seeds. The evidence suggested that *T. scrupulosa* had suppressed seeding by the untreated plants.

Quantitative assessment has been undertaken in current programs and detailed results from some are given in other papers in this Symposium. *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) which galls leaf- and flower-buds of *Baccharis halimifolia* L. (Compositae) has reduced the number of flower-bearing capitula by 93% in the vicinity of liberation sites (McFadyen 1985). Within 16 months of release, *Bruchidius sahlbergi* Schilsky (Coleoptera: Bruchidae), had destroyed up to 52% of the seeds of *Acacia nilotica indica* (Benth.) Brenan (Leguminosae) in plots fenced to exclude grazing stock (Willson 1985). *Erytenna consputa* Pascoe (Coleoptera: Curculionidae) has destroyed up to 82% of the seeds of *Hakea sericea* Schrader (Proteaceae) near liberation sites (Kluge 1984). A gall wasp, *Trichilogaster acaciaelongifoliae* (Froggatt) (Hymenoptera: Pteromalidae) has reduced seed production of *Acacia longifolia* (Andr.) Willd. by up to 99% after only two generations (G.B. Dennill, pers. comm.). For other seed-attacking

Table 1. Insects established to suppress reproduction of woody weeds.

Weed	Insect	Mode of attack	Region of introduction	Results
Anacardiaceae				
Schinus terebinthifolius Raddi	*Bruchus atronotatus* Pic (Coleoptera: Bruchidae)	Larvae feed in seeds[1]	Hawaii	Effects negligible[2]
Boraginaceae				
Cordia macrostachya (Jacq.) R. & S.	*Eurytoma attiva* Burks (Hymenoptera: Eurytomidae)	Larvae feed in seeds[1]	Malaysia	Contributing to control[2]
			Mauritius	Effective control[2] 16-81% seed destroyed; 50% island wide[1]
			Sri Lanka	Establishment unconfirmed[2]
Compositae				
Baccharis halimifolia L.	*Rhopalomyia californica* Felt (Diptera: Cecidomyiidae)	Gall leaf and flower buds	Queensland, Australia	Established[1]
Leguminosae				
Acacia longifolia (Andr.) Willd.	*Trichilogaster acaciaelongifoliae* (Froggatt)(Hymenoptera: Pteromalidae)	Gall leaf and flower buds	Cape P., S. Africa	Seeding reduced up to 99%[1,5]
A. nilotica indica (Benth.) Brenan	*Bruchidius sahlbergi* Schilsky (Coleoptera: Bruchidae)	Larvae feed in seeds	Queensland, Australia	Established[1]
Cytisus scoparius (L.) Link	*Apion fuscirostre* F. (Coleoptera: Curculionidae)	Larvae feed in seeds; adults on developing buds, flowers and pods[1]	California, USA	No noticeable control[2]
Mimosa pigra L.	*Acanthoscelides quadridentatus*	Larvae feed in seeds	N.T., Australia	Apparently established[1]

Table 1. Continued.

Weed	Insect	Mode of attack	Region of introduction	Results
	(Schaeffer) (Coleoptera: Bruchidae)			
	A. puniceus Johnson	Larvae feed in seeds	N.T., Australia	Apparently established[1]
Ulex europaeus L.	*Exapion ulicis* (Forster) (Coleoptera: Curculionidae)	Larvae feed in seeds[3]	Tas.,Vic., Australia	Little effect on spread[2]
			Hawaii	Negligible effect[3]
			N. Zealand	Seed reduced 20 to >90%. Aggressiveness checked[3]
			Cal., Or., USA	Considerable seed destruction. Reduced plant vigor at one site[3]
Melastomaceae				
Melastoma malabathricum L.	*Selca brunella* Hampson (Lepidoptera: Arctiidae)	Flower buds leaves, and terminals	Hawaii	Effects negligible[2]
Proteaceae				
Hakea sericea Schrader	*Carposina autologa* Meryick (Lepidoptera: Tortricidae)	Mature fruits	Cape P., S. Africa	Established[3]
	Erytenna consputa Pascoe (Coleoptera: Curculionidae)	Immature fruits	Cape P., S. Africa	Destroyed up to 82% of seed crop at study site[1,4]
Verbenaceae				
Lantana camara L.	*Epinotia lantana* (Busck) (Lepidoptera: Tortricidae)	Larvae mine shoots, recepticles	Qld., NSW, Australia	Minimal[2]

Table 1. Continued.

Weed	Insect	Mode of attack	Region of introduction	Results
		and fruit, and feed on flowers[3]		
	Ophiomyia lantanae (Froggatt) (Diptera: Agromyzidae)	Usually feed on endocarp[3]	Widespread	Minimal[2]
	Lantanophaga pusillidactyla (Walker) (Lepidoptera: Pterophoridae)	Flower buds, flowers & fruits[3]	Australia, Hawaii, Hong Kong	Minimal[2]
	Strymon bazochii (Godart) (Lepidoptera: Lycaenidae)	Flowers and immature fruits[3]	Fiji, Hawaii	Minimal[2]
	S. echion (L.)	Flowers and immature fruits	Hawaii	Minimal
	Teleonemia scrupulosa Stål (Hemiptera: Tingidae)	Flowers and foliage	Widespread	Can reduce seeding
	T. harleyi Froeschner	Flowers primarily	Queensland, Australia	Unknown

[1] Recent introduction; [2] Julien 1982; [3] Goeden 1978; [4] Kluge 1984; [5] G.B. Dennill (pers. comm.)

insects liberated against *H. sericea* and *Mimosa pigra* L. (Leguminosae) (Table 1) data are as yet unavailable. However in all these current programs work is under way to evaluate accurately the effects of introduced control agents which attack flowers or seeds and some important results should emerge.

Are Insects which Reduce Seeding Effective Biological Control Agents?

Huffaker (1964), citing Chater and Wilson, suggested that insects which damage only seeds of long-lived perennial weeds are normally not very suitable for introduction as biological control agents. He supported this opinion with the statement (p. 639) that 'The host persists and control is unlikely, especially as vegetative reproduction is common and some flowering is likely to occur during periods when the insects are inactive'. Clonal growth is in fact unknown in field populations of the woody weeds listed in Table 1 and, in programs for which figures are available, the amount of seed destroyed is *c.* 16–99%. This level of pre-dispersal loss of seed approximates the range of 10–90% quoted by Janzen (1971) as being normally encountered within the native range of many plants. When predators are freed from their natural control agents and introduced for biological control, seed losses may be in the upper part of this range.

Insects which destroy flower buds or flowers may lower the seed crop size, but frequently plants produce large numbers of flowers only to attract pollinators. Furthermore, the plant may partially compensate for attack on flowers by increased flower production. Compensatory growth may also follow damage to green fruits. On the other hand, plants cannot compensate for destruction of ripe seeds (Janzen 1971). The effects of flower (or bud) damage should not however, be underestimated. In other papers in this Symposium, McFadyen (1985) has described the interaction between *R. californica* and *B. halimifolia*, and Neser (1985) the interaction between *T. acaciaelongifoliae* and *A. longifolia*.

Regarding direct attack by insects on seeds, Southgate (1979) stated that most bruchids which have been studied were able to infest an exceedingly high proportion of the seeds on a plant. In some species of plants, the resultant destruction of seeds reduced the number of seedlings below that needed to maintain the plant population. However, the probability that seeds will be attacked by bruchids depends on the type of seed pod and whether it is still attached to the plant. Seeds from dehiscent pods of leguminous plants have a good chance of escaping predation by bruchids, whereas seeds from indehiscent pods are fed upon much more heavily when in pods on the plant than when they have fallen to the ground, and seeds from partially dehiscent pods are preyed upon more heavily on the ground than when in pods on the plant (Johnson 1981).

In another study, Center and Johnson (1974) observed that 72% of bruchid species attacking plants with indehiscent pods oviposited on the pod valve, not directly on the seed. They postulated that non-toxic, indehiscent, pod valves are attractive as food for vertebrates which act as dispersal agents for the seeds. Willson (1985) has discussed *B. sahlbergi* in another paper in this Symposium. *B. sahlbergi* attacks the seed of *A. n. indica*, a plant with a fleshy pod attractive to sheep as food. It appears that populations of this insect are to some extent regulated by sheep, which by eating the pods, both reduce the quantity of seed available and kill the larvae in infested seed. By contrast, populations of *Acanthoscelides* spp. (Coleoptera: Bruchidae), insects which attack the pods of *M. pigra*, are unlikely to be regulated in this way, as the pods of *M. pigra* are unattractive to vertebrates as food. In *M. pigra* the ripe, indehiscent joints break out and are dispersed by adhering to the fur of animals or, most frequently, floating on water (Miller 1983). As the indehiscent joints dry further, each becomes partially dehiscent. *Acanthoscelides* spp. oviposit in persistent sutures on the surface of the near-mature pod while still on the plant and, at least in the laboratory, also inside partially dehiscent joints not attached to the plant. These bruchids were first liberated in 1983 and it is too soon for the effects on the quantity of viable seed produced by *M. pigra* to be known. As they appear to be without parasites or predators in Australia the findings of Center and Johnson (1974) and Johnson (1981) suggest that very high levels of seed mortality may be expected.

Suppression of reproduction is important for control of woody weeds in three situations: (1) When the weed occupies only a portion of its potential range and is spreading by seed, suppression of reproduction will prevent or reduce spread; e.g. *M. pigra*; (2) When there is a conflict of interest and existing stands are of some benefit or use but an increase in their density, or in the area occupied, is undesirable; e.g. *A. n. indica*; and (3) When a weed may be easily killed by herbicide application but control is short-lived because of reinfestation by seeds and continued retreatment is uneconomical and/or environmentally undesirable; e.g. *B. halimifolia*.

Other factors which will influence the population density of plants in existing stands include the longevity and germination rate of seeds in the seed bank, and the mortality of seedlings and mature plants. Consideration of these factors is outside the scope of this paper.

Conclusions

The levels of flower and seed predation required to control weeds remains to be determined, but in the case of the annual herbaceous weed *Xanthium strumarium* L. (Compositae) in Australia, Holloway (1964) suggested that total seed destruction would be required to achieve control. Current research into the population dynamics of weeds, and quantitative evaluation of interactions between weeds and the insects which attack their flowers and seeds, will enable prediction of the levels of recruitment below which there is zero or negative population increase. The available evidence indicates that insects which destroy flowers and seeds may contribute substantially to reducing the population densities of woody weeds to economically acceptable levels.

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The Weed *Sesbania punicea* (Leguminosae) in South Africa Nipped in the Bud by the Weevil *Trichapion lativentre*

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Abstract

Sesbania punicea is a South American shrub that has invaded riverine habitats and is expanding its range throughout South Africa. During 1982, four weevil species from Argentina, *Trichapion lativentre*, *Rhyssomatus marginatus*, *Diplogrammus quadrivittatus*, and *Eudiagogus episcopalis*, were imported for screening as biocontrol agents against *S. punicea*. Recently, *T. lativentre* was found to be established on *S. punicea* in South Africa. Adults of *T. lativentre* are leaf-feeders. Larvae develop in flower buds and prevent seed-set. Preliminary surveys during the 1983/84 summer showed that: (a) *T. lativentre* was abundant and widespread in the eastern parts of the country; (b) in the hinterland, *T. lativentre* destroyed most flower buds and no seeds were set; and (c) along the coast, some seeds were produced, even where weevil densities were high. *T. lativentre*, supplemented by other agents, if necessary, should bring *S. punicea* under biological control in South Africa.

La Plante Nuisible *Sesbania punicea* (Légumineuse) d'Afrique du Sud Détruite au Stade de Bouriglon par le Charançon *Trichapion lativentre*

Sesbania punicea est un arbuste d'Amérique du Sud qui a envahi les habitats riverains et dont l'aire de distribution s'étend de plus en plus en Afrique du Sud. En 1982, quatre espèces de charançons d'Argentine, à savoir *Trichapion lativentre*, *Rhyssomatus marginatus*, *Diplogrammus quadrivittatus*, et *Eudiagogus episcopalis*, ont été importés afin d'être mis à l'assai comme agents de lutte biologique contre *S. punicea*. On vient de découvrir qui *T. lativentre* s'est établi sur *S. punicea* en Afrique du Sud. Les adultes de *T. lativentre* sont des insectes défoliateurs. Les larves se développent dans les bourgeons de fleurs et les empêchent de grener. Les études préliminaires effectuées pendant l'été 83 à 84 ont établi les conclusions suivantes: (a) *T. lativentre* était abondant dans les régions de l'est du pays où ses aires de distribution étaient vastes; (b) dans l'arrière pays, *T. lativentre* a détruit la majorité des bourgeons de fleurs et il n'y a eu aucun développement de graines; et (c) en bordure de la côte, certaines graines ont été produites, même dans les zones où les densités de charançons étaient fortes. L'introduction de *T. lativentre* et, au besoin, d'autres agents biologiques devrait permettre d'assurer une lutte biologique efficace contre *S. punicea* en Afrique du Sud.

Introduction

Sesbania punicea Benth. (Leguminosae) is a woody shrub that is native to Argentina, Uruguay and Brazil (Erb 1979). Approximately 25 years ago, *S. punicea* was introduced into South Africa, where it has since spread throughout the country, and has invaded disturbed areas and riverine habitats to the exclusion of indigenous vegetation. All parts of the plant, in particular seeds, have toxic properties that enhance its weed status. The spread of *S. punicea* has been greatly facilitated by its attractiveness as a garden plant and its efficient seed dispersal. Most pods drop from plants before releasing their seeds and, because plants often overhang flowing water (due to a high dependence on moisture for seed germination and growth), the buoyant pods are readily carried downstream for long distances.

Although *S. punicea* is widespread in South Africa and is still expanding its range, it has not yet achieved major economic importance. As a result, no herbicides have been registered for its control, and presently, the principal means of control is mechanical. This is only effective if the whole plant is uprooted and destroyed, making it very labour-intensive. These control limitations make *S. punicea* a particularly good candidate for biological control.

In 1982, four weevil species were collected in the Entre Rios Province of Argentina and imported into South Africa as potential biological control agents of *S. punicea*. They were the seed-feeder, *Rhyssomatus marginatus*, the stem-borer, *Diplogrammus quadrivittatus*, the root-feeder, *Eudiagogus episcopalis*, and the bud-feeder, *Trichapion lativentre*, which was subsequently found to be already well established in South Africa, over 1000 km from the quarantine facilities. The circumstances surrounding its introduction are obscure. Soon after its discovery in South Africa, surveys were conducted to determine the range over which *T. lativentre* had spread and to estimate the impact that the beetle was having on the reproductive potential of *S. punicea*. The results of these surveys are presented and discussed.

Biology of *T. lativentre*

Adults of *T. lativentre* feed on leaves of *S. punicea*, causing a shot-hole appearance of leaflets. Mating takes place soon after adult emergence and continues intermittently throughout the life of the adults (at least eight or nine months, since adults overwinter). Apparently, oviposition occurs whenever buds are available, although there appears to be a critical bud size of approximately 2 mm in length, below which the females will not oviposit. Larvae develop and pupate within the buds and adults emerge approximately 14 days after oviposition.

Sampling Methods

The impact of *T. lativentre* on the reproductive success of *S. punicea* was determined by measuring pod production by the plant in relation to density of adult weevils on plants at 11 different sites.

A box made from clear, expanded plastic, based on a design by Dempster (1961), was used to collect the weevils. The box is hexagonal in cross section (30 long × 13 wide × 11 cm deep). It is hinged along the longitudinal axis so that it can be opened into two halves and snapped shut around the branch to be sampled. Pyrethrum insecticide from an aerosol dispenser was sprayed into the chamber through a hole in one end of the box. This had a rapid 'knockdown' effect, and the dead beetles were then counted. Each sample collected the beetles that were present on the terminal 30 cm of the branch, corresponding to the length of the sampling device.

The number of pods and axils along the whole length of the sample branches were counted after the beetles had been removed. The number of pods/axil was then calculated to enable direct comparison of pod production on branches of different lengths. Any flower buds on these branches were collected and preserved for dissection, to determine the percent of buds in which oviposition had occurred.

Results and Discussion

Plants at three of the inland sites still had flower buds when first sampled in November 1983. Where beetle densities exceeded five adults/sample, almost 100% of the buds contained either eggs or larvae of *T. lativentre*. In terms of pod production

(Table 1), this meant that where the beetle densities had exceeded approximately two adults/sample, no pods were produced at the inland sites. However, at the coastal sites, pods developed on the plants even though beetle densities were higher than those at the inland sites.

The reasons for this difference are not clear but two possible explanations are: (1) the beetle numbers at the coast may have been much lower earlier in the summer when the plants were flowering and before any samples were taken; and (2) the earlier flowering season at the coast may have allowed pods to develop on the plants before the ovaries of the beetles matured following the winter dormancy.

To our knowledge, there is no record of a bud-feeding insect having yet been used for biological weed control (but see Neser 1985). Insects that reduce seed production are generally not considered to be successful control agents. A limitation often cited is that large seed banks in the soil may produce new plants for many years after the introduction of the agent. This should not be a problem with *S. punicea* because the seeds only remain viable in the soil for a maximum of two years (Graaff 1982). As a result, *T. lativentre* should have an immediate and lasting impact on the spread of *S. punicea*, providing the populations of the beetle remain at relatively high levels.

Table 1. *Sesbania punicea* Benth. pod production in relation to the density of adult *Trichapion lativentre*.

Location	Mean no. beetles/sample Nov. 1983	No. pods/[1] 100 axils
Inland Sites	0.0	79
	1.0	31
	1.5	51
	3.8	0
	4.4	0
	5.8	1
	17.3	0
Coastal Sites	0.0	47
	2.4	30
	5.2	3
	46.8	23

[1] Inland sites - Jan. 1984; Coastal sites - Nov. 1983.

Further surveys are planned for the 1984–85 summer to establish the cause of the better performance of *T. lativentre* at the inland sites. If *T. lativentre* is still unable to check the spread and increase of the plant along the coast, its action will be augmented by the release of other seed-feeding insects, such as *R. marginatus*. The existing stands of *S. punicea* will hopefully also be reduced through the action of the stem-boring weevil, *D. quadrivittatus*. Specificity tests on *R. marginatus* and *D. quadrivittatus* have been completed and both insects should be cleared for release by October 1984.

The prospects are excellent that *S. punicea* will be brought under biological control by *T. lativentre* in the near future, and before the plant has realized its full potential as a weed.

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The Role of Insects in the Long Term Control of *Opuntia aurantiaca*

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Abstract

Populations of *Opuntia aurantiaca* and their biological control agents were monitored, using fixed transects, over a five-year period. Insects reduced a moderate *O. aurantiaca* infestation at Tamworth to an acceptable level. *Dactylopius austrinus* was responsible for most of the decrease although *Cactoblastis cactorum* reduced some large clusters of plants. Abiotic causes, largely desiccation, were an important means of regulating scattered *O. aurantiaca* plants. It should be possible to control *O. aurantiaca* infestations in the survey area using existing insects, although redistribution of *D. austrinus* may be worthwhile after wet years.

Rôle des Insectes dans la Lutte à Long Terme Contre *Opuntia aurantiaca*

Des populations de *Opuntia aurantiaca* et les agents biologiques utilisés pour la lutte contre cette plante nuisible ont fait l'objet d'une surveillance dans des transects précis pendant une période de cinq ans. Les insectes ont réduit à un niveau acceptable une infestation modérée de *O. aurantiaca* à Tamworth. La majorité des mauvaises herbes ont été détruites par *Dactylopius austrinus*, bien que *Cactoblastis cactorum* ait éliminé de grandes touffes de plantes. Des facteurs abiotiques, principalement la dessication, ont joué un rôle important dans la lutte contre les plants épars de *O. aurantiaca*. Il devrait être possible de restreindre les infestations de *O. aurantiaca* dans le région de l'étude au moyen des insectes existants, bien qu'une redistribution de *D. austrinus* puisse être avantageuse après les années de fortes pluies.

Introduction

Opuntia aurantiaca Lindley (Cactaceae), tiger pear, is the major cactus pest in New South Wales. Infestations are largely confined to northeastern New South Wales inland from the Great Dividing Range and also to the Hunter Valley (Hosking and Deighton 1979). This cactus is a problem in grazing land where the barbed spines cause inconvenience and injury to stock and their handlers, and plants compete with useful pasture species.

Three insect species have been released for control of *O. aurantiaca*. *Cactoblastis cactorum* (Berg) (Lepidoptera: Phycitidae) was released in 1926, largely for control of *Opuntia stricta* (Haworth) Haworth varieties. *Dactylopius austrinus* De Lotto (Homoptera: Dactylopiidae) was released in 1933 and *Tucumania tapiacola* Dyar (Lepidoptera: Phycitidae) in 1935. These two species were specifically released for *O. aurantiaca* control.

This paper shows how insects and climatic conditions affect a field infestation of *O. aurantiaca*.

Methods and Materials

The site of these experiments was hilly grazing land near Tamworth (31°07'S, 151°04'E). The area had a long history of attempts to eradicate *O. aurantiaca* using chemicals. Insects which damage *O. aurantiaca* had been released in the area, probably as early as the mid-1930s. *D. austrinus*, *C. cactorum* and *T. tapiacola* were present at the commencement of these experiments and no attempt was made to assist their dispersal at any stage of the experiments.

In 1979, 10 randomly chosen permanent transects were set up. These transects were inspected at approximately three-monthly intervals from May 1979 to May 1983. Transects were 2 m wide and 50 m long. The method used to follow *O. aurantiaca* plants and their biological control agents in these transects was devised by Zimmermann (1977). Plants were separated into four categories: (a) loose segments (category A); (b) small plants with roots, 1–4 segments (category B); (c) medium-sized plants, 5–10 segments (category C); and (d) large plants with >10 segments (category D). Each transect was divided into 100 square meters (quadrats) and the history of each square meter was followed over a four-year period. Inspections were made by spreading a chain, marked at meter intervals, along the length of each transect. A metal frame, made up two separate meter squares, was bolted together and placed over the chain to facilitate observation of meter squares on each side of the chain. For each square meter, records were made of the number and category of plants present and presence or absence of various biological control agents. Two people carried out inspections, one working on either side of the transect.

Table 1. Percent ground cover according to a modified Domin scale.

Percent ground cover	Rank
0	0
present <0.5	1
0.5 < 2	2
2 < 5	3
5 < 10	4
10 < 20	5
20 < 33	6
33 < 50	7
50 < 75	8
75 <100	9
100	10

Ground cover was also followed using a modified Domin scale (Table 1). An overall value for percent ground cover, for each sampling period, was obtained by converting rankings back to percent ground cover. To obtain this figure, the mid-value for percent ground cover for each rank was multiplied by the number of times that rank occurred, and values were summed for all ranks.

Analyses (Nelder and Wedderburn 1972) were carried out to determine whether increases or decreases in percent ground cover between sample dates were related to presence of biological control agents on the earlier date. Rankings of 0 and 1 were not considered, as small amounts of *O. aurantiaca* were easily overlooked.

An intensive sampling programme was begun in mid-1982 to accurately record causes of increase and decrease in numbers of *O. aurantiaca* segments. For this purpose 10 smaller permanent transects, each 10 × 1 m were checked at 2–4-wk intervals,

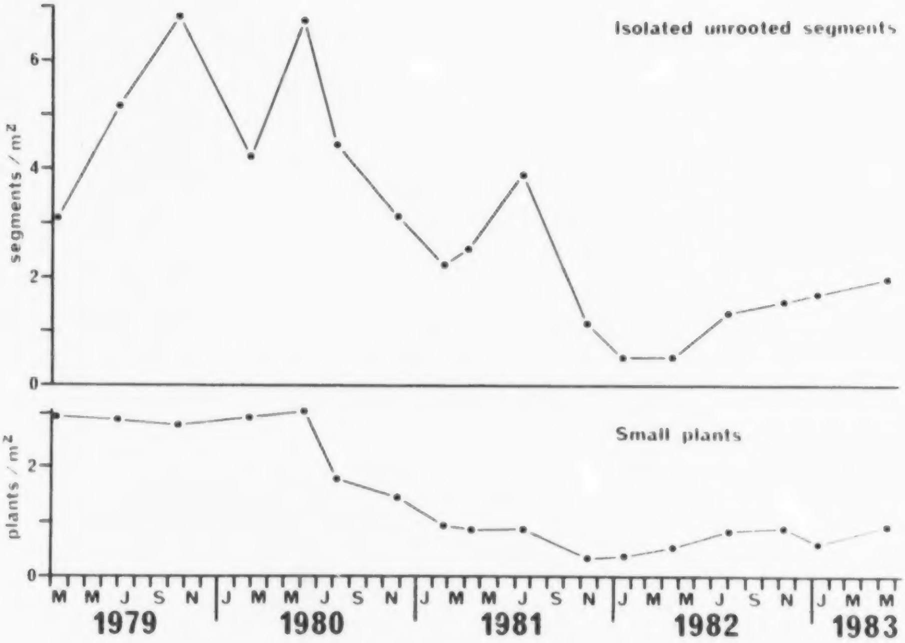

Fig. 1. Fluctuations in the number of isolated unrooted *Opuntia aurantiaca* Lindley segments and small *O. aurantiaca* plants at Tamworth, N.S.W. (March 1979–March 1983).

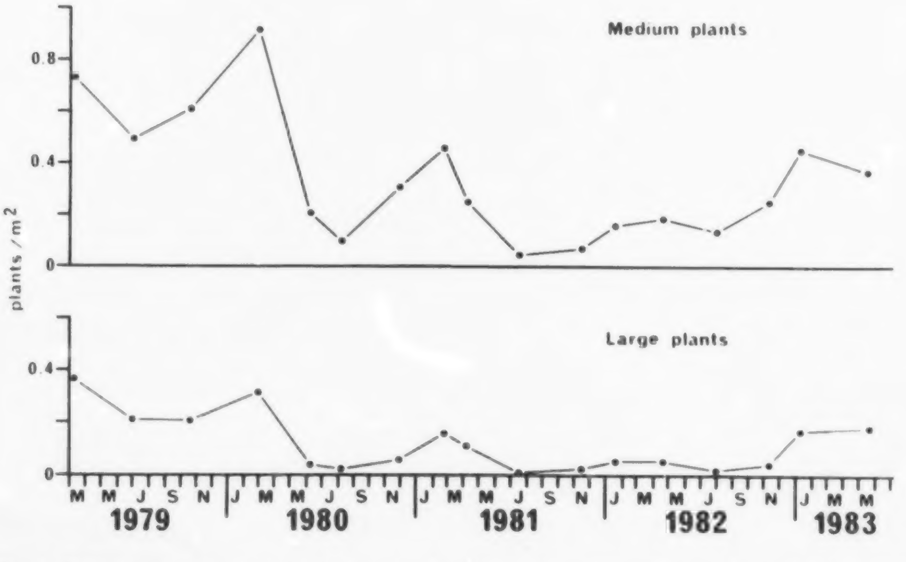

Fig. 2. Fluctuations in the number of medium and large *Opuntia aurantiaca* Lindley plants at Tamworth, N.S.W. (March 1979–March 1983).

observations being more frequent in warmer months. These transects had previously been used to follow populations of *O. aurantiaca* and biological control agents (unpubl. data), but these records did not include causes of increase and decrease within each transect. The need for a detailed survey was made apparent while visiting Dr. H. Zimmermann in South Africa during 1982. He had found that desiccation was an important cause of decrease in *O. aurantiaca* populations (Zimmermann 1981).

Rainfall and temperature were obtained on site for the duration of all experiments.

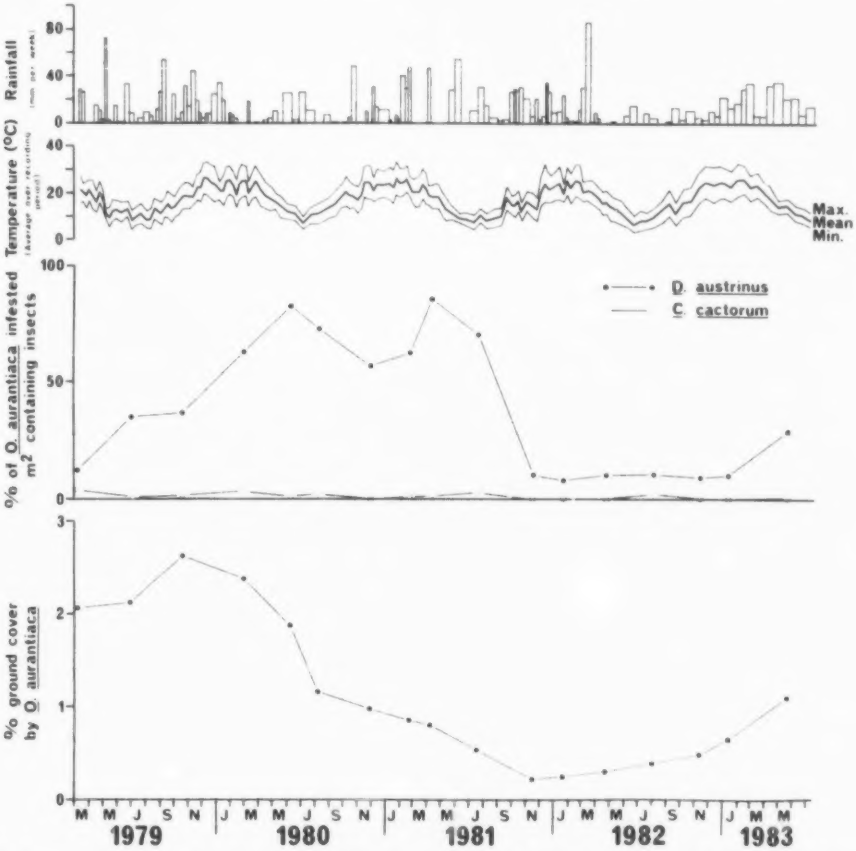

Fig. 3. Ground cover by *Opuntia aurantiaca* Lindley, percent *Dactylopius austrinus* De Lotto and *Cactoblastis cactorum* (Berg) infestation of *O. aurantiaca* and weather data recorded at Tamworth, N.S.W. (March 1979–March 1983).

Results and Discussion

Numbers of *O. aurantiaca* plants and segments varied greatly over the experimental period (Figs. 1, 2). Higher numbers of larger plants (C, D) were present between January and March each year compared with other months. This corresponds to the time when *O. aurantiaca* plants are growing new segments (see below).

The percent of ground covered by *O. aurantiaca* varied from 2.6–0.2% (Fig. 3). The changes did not follow the trend in numbers of medium (C) and large (D) plants but rather a combination of the numbers of smaller (B) plants and loose segments (A).

D. austrinus numbers increased from being present in 12% of quadrats containing *O. aurantiaca* in May 1979, to being present in 86% of quadrats containing *O. aurantiaca* in April 1981 (Fig. 3). This period of *D. austrinus* increase corresponds with the large drop in % ground cover by *O. aurantiaca* (Fig. 3). Table 2 shows how much of the decrease appears to be attributable to *D. austrinus*. *C. cactorum* also lowered % ground cover by *O. aurantiaca* on most occasions when it is present. *T. tapiacola* was rarely found at this site so the effect of this insect was ignored.

Table 2. Percent of *Opuntia aurantiaca* Lindley infested quadrats containing *Dactylopius austrinus* De Lotto, at the beginning of the sampling period, in relation to change in *O. aurantiaca* ground cover over the sampling period. The sample area at Tamworth consisted of 1000 square m quadrats.

	% of *O. aurantiaca* infested quadrats containing *D. austrinus* at the beginning of the sampling period		
Sampling Period[1]	No change in cactus cover[2] Mean (*SE*[3])	Increase in cactus cover[2] Mean (*SE*[3])	Decrease in cactus cover[2] Mean (*SE*[3])
Mar.-June	62.65 (14.90)	39.02 (29.93)	84.40 (10.07)
June-Sept.	61.73 (15.17)	65.16 (26.05)	80.99 (12.11)
Sept.-Dec.	53.96 (15.92)	48.62 (25.30)	69.10 (16.66)
Dec.-Mar.	63.95 (13.87)	32.45 (23.19)	74.30 (15.71)

[1] Approximate sample periods.

[2] Rankings of 0 and 1 (0 to <0.5% ground cover) at the beginning of the sampling period have not been included.

[3] These were obtained by multiplying the standard error from the assumption of binomal errors by the square root of the residual mean deviance, since this figure exceeds 1.

Table 3. A summary of factors affecting the number of *Opuntia aurantiaca* Lindley segments in a 100 square m sampling area at Tamworth (733 segments being present of 24.vi.1982).

Factor	24.vi.1982 to 24.vi.1983	24.vi.1983 to 22.vi.1984
Increase		
New growth	1521	1620
Brought in	172	119
Found	171	154
TOTAL	1864	1893
Decrease		
Not found	169	47
Rot	12	31
Removed	410	295
Cactoblastis cactorum Berg.	21	0
Dactylopius austrinus De Lotto	131	46
Abiotic - largely desiccation	459	92
TOTAL	1202	511

Rainfall was lower than average for most of the period from May 1979 to May 1983 (Fig. 3). This was an important factor in the decrease in % ground cover by *O. aurantiaca* and the subsequent maintenance of cactus at this level. Moisture stress, which occurred frequently over this period, has been shown to accelerate death of *O. aurantiaca* infested with *D. austrinus* (Hosking and Deighton 1981). Moran and Annecke (1979) also reported that *D. austrinus* is a more effective natural enemy of *O. aurantiaca* under dry conditions. Although *D. austrinus* populations decreased to low levels once a large proportion of *O. aurantiaca* was dead, numbers and size of cactus plants failed to increase until good rains occurred during the growing period.

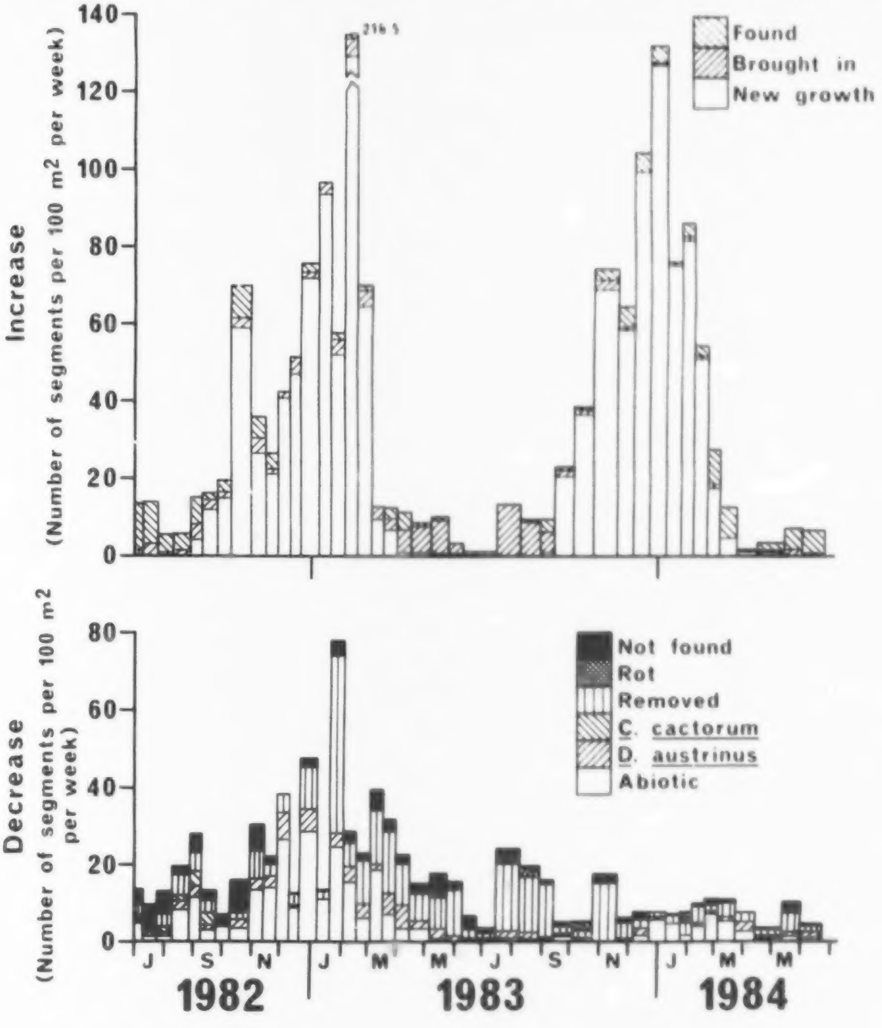

Fig. 4. Causes of increase and decrease in a population of *Opuntia aurantiaca* Lindley at Tamworth, N.S.W. (June 1982–June 1984).

Good rains fell in January 1983 and this corresponds to the period when the cactus population began to increase.

Intensive sampling (Fig. 4, Table 3) was carried out from mid-1982 to mid-1984. New growth was the major cause of increase in numbers of *O. aurantiaca* segments in the sample area. This increase was greatest during the warmer months, growth beginning in late August and finishing during April the following year. During 1982–83 growth was greatest in February following good January rains but a peak in December–January, which occurred the following year, is likely to occur when good rains fall evenly over the warmer months. Smaller numbers of segments were brought into or found within transects during the sampling period. Animals brought in some segments while others fell into transects from plants rooted outside. Heavy rain also washed segments into transects when the ground was largely bare. The 'found' category includes segments which were brought into the area but not found until they had grown into small plants.

Abiotic death, largely due to desiccation, was the main cause of decrease during 1982–83 but was less important in 1983–84. This could largely be explained by rainfall (Fig. 5). Periods of high rainfall corresponded with low amounts of *O. aurantiaca* death due to desiccation. A large number of segments were not found during sampling. These may have been removed or died but no trace of animal movement or dead segments was present near past segment locations. The 'removed' category may also be too high, probably including some abiotic and insect-related death. However, transects were originally set up in areas of high cactus density (in 1979) and these areas still, in general, contain more segments than surrounding areas. Removal would therefore be expected to exceed the number of segments brought into transects (this would include numbers of segments in the 'brought in' as well as part of the 'found' categories). *D. austrinus* death was greater in the drier year. The reason for this was explained earlier. Rotting of *O. aurantiaca* segments was greater in wet periods but still only accounted for a small amount of *O. aurantiaca* death in either year.

Fluctuations in the *O. aurantiaca* population at the study site can be explained by climatic conditions and insect-related damage (Figs. 3, 4, 5). In 1979, when these experiments began, the *O. aurantiaca* population was considered to be reaching problem proportions and would soon need treatment. Dry conditions began late in 1979, and this, together with a rapid build-up in the *D. austrinus* population, resulted in a large decrease in numbers and size of *O. aurantiaca* plants. By mid- to late-1980, treatment was no longer considered necessary. As this and similar experiments at other locations have continued it has become increasingly obvious that the level at which *O. aurantiaca* causes an economic problem needs to be accurately defined.

Biological control of *O. aurantiaca* by *D. austrinus* appears to be adequate under dry conditions. The rate at which control can be achieved following wet periods can be increased by hand spreading of *D. austrinus* infested segments (unpubl. data). Natural means of dispersal are often a factor limiting the level of control achieved by this insect (Moran and Annecke 1979). Wind dispersal of first-instar crawlers is normally the major means of *D. austrinus* dispersal. Without assistance *D. austrinus* spread can be patchy and slow. The economics of more rapid control through hand spreading of *D. austrinus* should be studied to determine whether this approach is worthwhile. Adequate control was achieved in this area without any additional distribution of *D. austrinus*.

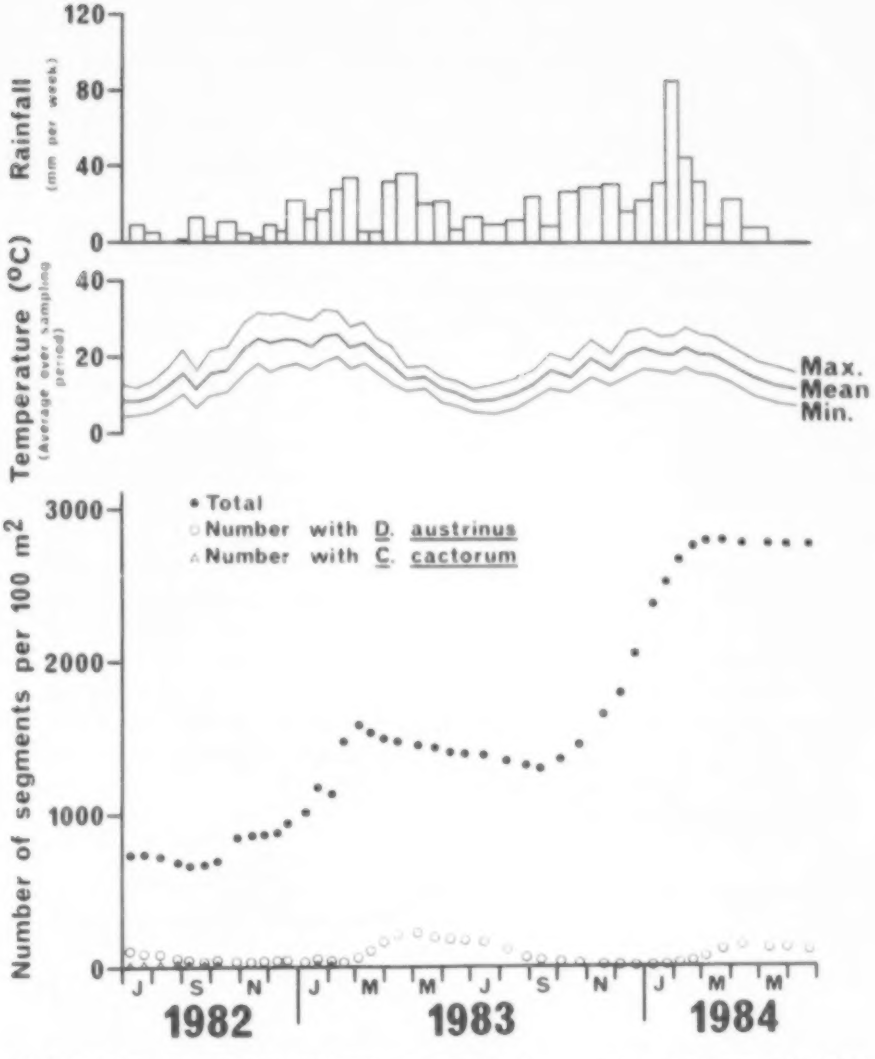

Fig. 5. Fluctuations in the number of *Opuntia aurantiaca* Lindley segments and segments with biological control agents in relation to climatic data, in a 100 m^2 sampling area at Tamworth, N.S.W. (June 1982–June 1984).

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Biocontrol Agents for *Parthenium hysterophorus* from Mexico

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Abstract

Parthenium hysterophorus (Compositae) is an opportunistic annual weed native to Mexico, which has been introduced into a number of tropical and subtropical countries and has become a particularly serious problem in Queensland (Australia) and in India. A five-year study in Mexico was conducted by the Commonwealth Institute of Biological Control on behalf of the Queensland Department of Lands, and as a result six species of insects were sent to Queensland for trial as biocontrol agents. These are a seed-feeding weevil (*Smicronyx lutulentus*), a defoliating chrysomelid (*Zygogramma bicolorata*), a stem-gall-forming tortricid (*Epiblema strenuana*), a delphacid plant-hopper (*Stobaera concinna*), a leaf-mining moth (*Bucculatrix* sp. 'D') and a root-feeding weevil (*Thecesternus hirsutus*). Brief details are given of the biology and effects on the plant of each of these species. All except *T. hirsutus* have now been released in Queensland. Several diseases of *P. hysterophorus* were also found including a rust caused by *Puccinia abrupta* var. *partheniicola*, and this appears to be worth further investigation.

Agents Biologiques de Lutte Contre *Parthenium hysterophorus* du Mexique

Parthenium hysterophorus (Composées) est une plante nuisible annuelle opportuniste d'origine mexicaine, qui a été importée dans un grand nombre de pays tropicaux et sub-tropicaux, et qui pose des problèmes particulièrement graves dans l'État de Queensland (Australie) et en Inde. L'Institut du Commonwealth pour la lutte biologique a mené une étude de cinq ans au Mexique pour le compte du Department of Lands (ministère des Terres) de Queensland et, comme résultat, il a envoyé espèces d'insectes à Queensland pour qu'elles soient essayées comme agents de lutte biologique. Il s'agit d'un charançon granivore (*Smicronyx lutulentus*) d'une chrysomèle défoliatrice (*Zygogramma bicolorata*), d'une tortricide provoquant la galle des tiges (*Epiblema strenuana*) d'une cicadelle delphacide (*Stobeara concinna*), d'un lépidoptère mineuse des feuilles (*Bucculatrix* sp. 'D') et d'un charançon racidivore (*Thecesternus hirsutus*). Le rapport donne quelques détails sur la biologie de chacune de ces espèces d'insectes et sur leurs effets sur la plante. Toutes les espèces ont actuellement été libérées à Queensland, sauf *T. hirsutus*. Plusieurs maladies s'attaquant à *P. hysterophorus*, dont une rouille causée par *Puccinia abrupta* var. *partheniicola*, ont été relevées, et il semble approprié de poursuivre les recherches.

Introduction

The annual weed *Parthenium hysterophorus* L. (Compositae), native to Mexico and the southern U.S.A., was introduced to Queensland, Australia, in the 1950s and now infests thousands of square km in the State (Haseler 1976; McFadyen 1984). These infestations occur mainly in grazing land in central Queensland, where the plant persists in dense monospecific stands, excluding beneficial pasture species. Its persistence is aided by its profuse seed production and ability to germinate at any time when temperature and moisture conditions allow. Extensive infestations of *P. hysterophorus* also occur in

India, and it is reported from tropical and subtropical areas of a number of other countries (Towers *et al.* 1977).

From 1978–83, the Commonwealth Institute of Biological Control carried out studies of the natural enemies of *P. hysterophorus* in north-eastern Mexico on behalf of the Queensland Department of Lands. A preliminary report on these studies was presented by McClay (1981). By 1983, 109 species of phytophagous arthropods had been identified feeding on *P. hysterophorus* in Mexico, biological and host-specificity studies had been carried out on 22 of these, and 6 species had been shipped to Queensland as candidate biocontrol agents (McClay 1983*a*). Five of these have now been released, and the results of the field release program are reported by McFadyen (1984). This paper describes the biology, host-specificity and effects on the host-plant of these six species.

Some observations were also made on pathogens attacking *P. hysterophorus*, and preliminary studies on some of these were made by Dr. H.C. Evans of the Commonwealth Mycological Institute during a visit to Mexico from March–May 1983 (Evans 1983). The most damaging pathogen observed was a rust fungus, *Puccinia abrupta* Diet. & Holw. var. *partheniicola* (Jackson) Parmelee (Uredinales). This species produces abundant telia and urdeinia which occur on leaves, stems and flowers. It occurs mainly in more elevated areas of north-eastern Mexico where there is a well-defined cool season. Field observations and preliminary tests suggest that this rust is specific to *P. hysterophorus*, and it merits further study as a possible biocontrol agent.

Materials and Methods

A base for the project was selected at Monterrey, Nuevo Leon, in facilities kindly made available by the Instituto Tecnologico y de Estudios Superiores de Monterrey (ITESM). The selection of this area was based upon the known distribution of *P. hysterophorus* and other *Parthenium* species in Mexico, and its climatic similarity to the infested areas of Queensland. *P. hysterophorus* is abundant in north-eastern Mexico, and several other species of the genus also occur in the region (Rollins 1950) suggesting that this is a centre of diversification for *Parthenium*. The climatic similarity can be seen in Fig. 1, which shows climate diagrams for Apodaca, Nuevo Leon (near Monterrey, and the site of the ITESM field station where experimental plots of *P. hysterophorus* were set up) and Emerald, Queensland (located in the *P. hysterophorus*-infested area of Queensland). Both locations receive around 630 mm of precipitation/year, occurring mainly in the summer. Both experience mean summer temperatures around 28°C and mean winter temperatures around 14°C, with occasional frosts in winter. Considerable year-to-year fluctuation in the total amount and seasonal distribution of rainfall is also a feature of both sites. The criteria for selection of areas for exploration for biological control agents for weeds (Wapshere 1981) were thus fulfilled.

The methods used were described in the previous report (McClay 1981) and will thus only be briefly summarized here. Collections of natural enemies were made on naturally occurring stands of *P. hysterophorus*, mainly in north-eastern Mexico but also in other areas. Periodic sampling on plots sown with *P. hysterophorus* at Apodaca, N.L., was carried out to provide information on the phenology of some of the main natural enemies.

Host-specificity testing was carried out mainly by means of multiple-choice tests in cages (1 high × 1 × 0.80 m). The test plants used included economic Compositae and species in several genera of the tribe Heliantheae, to which *Parthenium* belongs (Table 1). Particular importance was given to testing against sunflower (*Helianthus annuus*

L.; Compositae), an important crop plant closely related to *P. hysterophorus*, and against guayule (*Parthenium argentatum* A. Gray), a rubber-yielding species regarded as a potential crop in Australia. These tests were supplemented by field observations and literature searches. Species which gave indications of sufficient host-specificity in these tests were then sent to the Sir Alan Fletcher Research Station of the Department of Lands in Sherwood, Queensland, where extensive testing was carried out under quarantine against a wide range of economic plants.

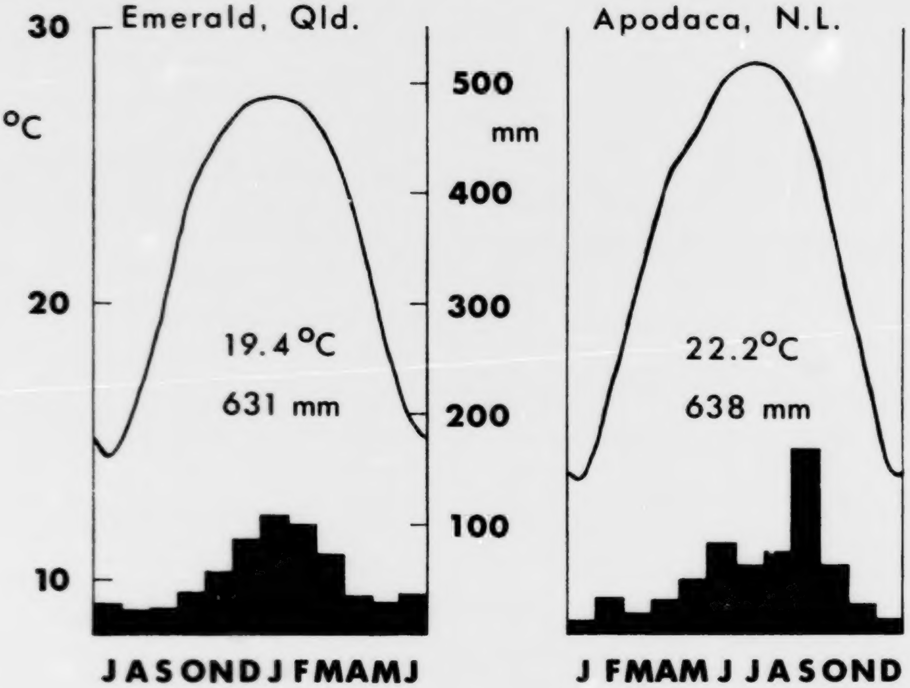

Fig. 1. Climate diagrams for Emerald, Queensland, and Apodaca, Nuevo Leon. Curves: mean monthly temperature (°C). Histograms: mean monthly precipitation (mm). Figures below curves: mean annual temperature and precipitation.

Results and Discussion

Smicronyx lutulentus *Dietz (Coleoptera: Curculionidae)*

This small weevil lays eggs in the young flower buds of *P. hysterophorus*, and larvae feed inside developing seeds. It is bivoltine in north-eastern Mexico, overwintering as larvae in the soil. The first generation of adults usually appears in May, and the second in late August or early September. After the appearance of the second generation the adults are often abundant on *P. hysterophorus*. This species may cause up to 30% seed destruction in the field in Mexico. The larvae are parasitized by *Zatropis* sp. nr. *incertus* Ashmead (Hymenoptera: Pteromalidae) and *Paracrias* sp. (Hymenoptera: Eulophidae). Tests showed that *S. lutulentus* is highly host-specific, feeding and ovipositing only in *P. hysterophorus* and the closely related *P. confertum* Gray, and its release in Australia has been approved.

Zygogramma bicolorata *Pallister (Coleoptera: Chrysomelidae)*

This leaf beetle, initially identified as *Zygogramma* sp. v. nr. *malvae* Stål, is common on *P. hysterophorus* in Nuevo Leon. It was also collected in a wide range of habitats from humid tropical lowlands in Veracruz to the arid central plateau in San Luis Potosi. Adults and larvae both feed on the foliage of *P. hysterophorus*, and when populations are high can cause considerable defoliation in the field. There are probably 2–3 generations during the summer; overwintering occurs as adults in the soil, although if fresh *P. hysterophorus* foliage is available, some adults may remain feeding on the plant until January or February. Host-specificity testing showed that in addition to *P. hysterophorus* and *P. confertum*, development can also be completed on *Ambrosia confertiflora* DC. (Compositae). Development on this host, however, is considerably slower than on *P. hysterophorus*. Slight adult and larval feeding also occurred on sunflower (*H. annuus*) in tests, but development cannot be completed on this plant. *Z. bicolorata* has the highest fecundity of any of the agents discussed here, producing a mean of 836 eggs/female. It has been approved for release in Australia, and is established in Queensland (McFadyen 1984). *Z. bicolorata* has also been shipped to India.

Table 1. Species of Compositae used in preliminary screening of candidate biological control agents for *Parthenium hysterophorus* L. in Mexico.

Species	Tribe	Status
Ambrosia confertiflora DC.	Heliantheae	Weed
Bidens pilosa L.	Heliantheae	Weed
Carthamus tinctorius L.	Cynareae	Economic
Chrysanthemum morifolium Ramat.	Anthemideae	Ornamental
Cichorium intybus L.	Cichorieae	Economic
Coreopsis lanceolata L.	Heliantheae	Ornamental
Cosmos bipinnatus Cav.	Heliantheae	Ornamental
C. sulphureus Cav.	Heliantheae	Ornamental
Dahlia coccinea Cav.	Heliantheae	Ornamental
Helianthus annuus L.	Heliantheae	Economic
H. ciliaris DC.	Heliantheae	Weed
Heliopsis sp.	Heliantheae	Weed
Lactuca sativa L.	Cichorieae	Economic
Parthenium argentatum Gray	Heliantheae	Economic
P. confertum Gray	Heliantheae	Weed
Rudbeckia serotinia Nutt.	Heliantheae	Ornamental
Viguiera dentata Cav. & Spreng.	Heliantheae	Weed
Xanthium chinense Mill.	Heliantheae	Weed
Zinnia elegans Jacq.	Heliantheae	Ornamental

Epiblema strenuana *(Walker) (Lepidoptera: Tortricidae)*

The larvae of this moth, which is sometimes abundant in Mexico, form large galls in stems and growing points of *P. hysterophorus*, which can severely stunt the growth of the plant, and thus limit flower and seed production. Plants attacked in the rosette stage or as the stem begins to elongate can be converted into distorted masses of gall tissue, which almost completely fail to flower. In Mexico the moth has 2–3 generations in the summer and overwinters as prepupal larvae (McClay, *in press*). Host-specificity tests and literature records show that, as well as *Parthenium*, it will attack and develop on species of *Ambrosia* and *Xanthium*. However, as these genera are represented in

Australia only by introduced weeds, and as they are closely related to *Parthenium*, the field release of this species was authorized. The establishment of *E. strenuana* in Queensland and its effects on *P. hysterophorus* there are reported by McFadyen (1984).

Stobaera concinna *(Stål) (Homoptera: Delphacidae)*

Work on this plant-hopper was prompted by the desire to find a vector for a phyllody disease of *P. hysterophorus* caused by a mycoplasm (Phatak *et al.* 1975). The disease causes sterility of affected flower heads, and was previously ascribed (McClay 1981) to the attack of a mite, *Eriophyes parthenii* Keifer (Acarina: Eriophyidae); this, however, has now been shown not to be the causal agent. The mycoplasm is already present in Queensland, but disease incidence is low. It was hoped that incidence could be increased by the introduction of a vector specific to *P. hysterophorus*. As most known vectors of plant mycoplasms are Homoptera, a series of species of this group found associated with *P. hysterophorus* was screened. Most were easily shown to be insufficiently host-specific, the exception being *S. concinna*. An attempt to show transmission of the disease by *S. concinna* was unsuccessful, but it was decided to proceed with the introduction of this species on the basis that: (a) the possibility of its being a vector had not been eliminated; and (b) it might prove damaging to *P. hysterophorus* in its own right.

S. concinna is rare on *P. hysterophorus* in the field in Mexico, and does not cause observable damage (McClay 1983*b*). In cages, however, it breeds readily on this host, rapidly building up dense populations which cause yellowing of the leaves and generally reduced vigor. It also breeds on *A. confertiflora*, but no breeding occurred on any of the other composites tested, and females confined on them failed to mature eggs. It therefore resembles *E. strenuana* and *Z. bicolorata* in its host range, and its release in Australia has been approved.

Bucculatrix *sp. 'D' (Lepidoptera: Lyonetiidae)*

The larvae of this small moth mine the leaves of *P. hysterophorus* in the first two instars and then emerge to feed externally on the leaves. It appears to be an undescribed species, as it does not agree with any named material in the British Museum (Natural History) or the U.S. National Museum, or with any of the species described by Braun (1963). It is provisionally referred to by the letter 'D', to distinguish it from other *Bucculatrix* species which were present in the same batch of material sent for identification.

This species is also scarce in the field, and field-collected larvae are frequently parasitized. In cages, it breeds readily on *P. hysterophorus*, and builds up high population densities, causing fairly heavy defoliation. In host-specificity tests, no attack occurred on any species outside the genus *Parthenium*. Occasional slight feeding occurred on *P. argentatum* in some tests, but this is thought to have been due to larvae transferring to this plant after initially feeding on *P. hysterophorus*. No evidence of oviposition or mining on *P. argentatum* was found. Some doubt persisted as to the possibility of attack on *P. argentatum*, as a few adults and larvae found in the field on this species appeared to be of *Bucculatrix* sp. 'D'. Further tests were therefore conducted in Mexico and subsequently in Queensland, and these showed that, at least as far as the particular population which was shipped to Queensland is concerned, *Bucculatrix* sp. 'D' shows no tendency to attack *P. argentatum*. Its release in Australia has therefore been authorized.

Thecesternus hirsutus *Pierce (Coleoptera: Curculionidae)*

The larvae of this large weevil feed externally on the roots of *P. hysterophorus*, on which they produce a gall-like swelling (McClay and Anderson, *in press*). The adults feed on the foliage. It is locally common in north-eastern Mexico, usually in dry, relatively undisturbed sites. The adults are flightless and long-lived, and there is a single generation/year, with possibly a partial second generation over the summer. Overwintering occurs as mature larvae.

This group of weevils has been little studied, and almost no information on its biology could be found. The only information on food habits which could be found in the literature was a 19th-Century reference to feeding by the adults on grape blossoms. This was not confirmed in tests carried out in Mexico. Field observations and laboratory tests showed that its host-range is restricted to a few closely related species in the genus *Parthenium*.

Despite its specificity, this insect is not regarded as a highly promising biological control agent for *P. hysterophorus*. The larval feeding affects only the cortical tissues of the root, and thus is unlikely to reduce significantly the plant's water uptake. Defoliation caused by the adults is very light. The insect's long life cycle and low reproductive rate would also limit its effectiveness as a biocontrol agent. It is possible that heavy root galling on young plants might be a sufficient metabolic sink to inhibit their growth and seed production.

T. hirsutus was, however, the only root-feeding insect found on *P. hysterophorus* in Mexico which could be recommended for further study in Queensland. Other root-feeding Coleoptera and Lepidoptera were either insufficiently specific, could not be reared in the laboratory, or were too scarce to be studied. A shipment of *T. hirsutus* was therefore sent to Sherwood for further host-range testing in quarantine. Owing to difficulties with rearing, however, the tests with this species were not completed and application for permission to release it in Australia was not made.

Discussion

The studies reported here have made available a complex of biocontrol agents for *P. hysterophorus*, which includes a seed-destroyer, a gall-former, a defoliator, a leaf-miner/defoliator, a sucking insect and an external root feeder. Some of these are specific to *P. hysterophorus* and one or two other closely related *Parthenium* species, while others will also attack *Ambrosia* spp. As far as introduction into Australia is concerned, attack on *Ambrosia* is not a problem, as this genus is represented there only by undesirable, introduced weeds. This applies also to the ability of *E. strenuana* to attack *Xanthium* spp. (McFadyen 1984).

The availability of a complex of biocontrol agents with different modes of attack is encouraging, as it has frequently been suggested that successful biological control is more likely where a number of different types of stress can be applied simultaneously to the target weed (Harris 1979; Haseler 1981).

On a subjective assessment, the most damaging of the agents discussed here is *E. strenuana*, as attack can occur at any growth stage of the weed, and a single, well-placed gall can be highly effective in restricting growth and hence seed production. *Z. bicolorata* is also regarded as promising because of its high fecundity, high consumption of foliage by both adults and larvae, and the wide range of environments in which it occurs in Mexico.

To assess the potential of the biocontrol agents discussed here, each agent was scored according to the scheme of Harris (1973) and the revised version of this scheme published by Goeden (1983). Where ambiguity or lack of information resulted in doubt as to what score should be assigned to a particular agent under a particular category, both possible scores were assigned and the results presented as the range of lowest to highest possible total scores. In order not to bias the scores in favour of earlier-released agents, no information derived from field release experience in Queensland was incorporated into the scores.

The results are shown in Table 2. Both schemes produce an essentially similar ranking of the six agents, and agree with the intuitive assessment in making *E. strenuana* the most promising agent and *T. hirsutus* the least. A surprising feature is the high ranking given to *S. concinna* by both schemes, particularly as it was not assumed that this species is a vector for the mycoplasm which causes phyllody of *P. hysterophorus*. If *S. concinna* were to be shown to transmit this disease, its score under both schemes would be further boosted.

Table 2. Scores assigned to biocontrol agents for *Parthenium hysterophorus* L. from Mexico according to the schemes of Harris (1973) and Goeden (1983)

Agent	Harris Score	Goeden Score
Epiblema strenuana (Walker)	23-30	53-57
Stobaera concinna (Stål)	18-22	42-48
Zygogramma bicolorata Pallister	20	43
Smicronyx lutulentus Dietz	18	43
Bucculatrix sp. "D"	11-17	36-45
Thecesternus hirsutus Pierce	7-13	32-39

Whether these scores accurately reflect the real potential of these insects for control of *P. hysterophorus* will be shown only by further experience with field releases. For the present it is recommended that consideration should be given to release of any or all of these species, but especially *E. strenuana*, in any area where *P. hysterophorus* is an important introduced weed.

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Introduction of the Gall Fly *Rhopalomyia californica* from the U.S.A. into Australia for the Control of the Weed *Baccharis halimifolia*

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Abstract

Baccharis halimifolia (Compositae) is a woody shrub native to the eastern coast of North America and is a serious weed in cattle pastures in Eastern Australia. In an attempt to control *B. halimifolia*, the gall fly *Rhopalomyia californica* (Diptera: Cecidomyidae) was introduced from California where it was collected from *B. pilularis*. In 1982, releases were commenced and the gall fly has established at most sites. Although there has been some attack by native parasites and predators, this is lower than the rate of increase. It has spread more than 10 km in 18 months and has stopped *c.* 90% of seeding at a heavily infested release site. This is highly significant as the massive annual production of wind-borne seed is one of the principal reasons why this plant is a serious weed. At this stage, it appears that the gall fly will give significant control of the weed, but it is still too early to know the long term effects on the plants and the degree of control that will finally be achieved.

Introduction de la Mouche Gallicole *Rhopalomyia californica* des États-Unis en Australie pour la Lutte Biologique Contre la Plant Nuisible *Baccharis halimifolia*

Baccharis halimifolia (Composée) est un arbuste ligneux indigène de la côte est de l'Amérique du Nord qui est très nuisible dans les pâturages du bétail dans l'est de l'Australie. Pour essayer de lutter contre *B. halimifolia*, la mouche gallicole *Rhopalomyia californica* (Cecidomyidés) a été importée de Californie où elle a été recueillie sur *B. pilularis*. En 1982, les lâchers ont commencé et les mouches gallicoles se sont établies dans la plupart des sites. Les galles ont atteint les extrémités des jeunes plants en croissance et des plants matures, ce qui a détruit environ 90% des graines. Il s'agit d'un succès exceptionnel puisque la production annuelle massive de graines disséminées sous l'action du vent est l'une des principales raisons pour lesquelles cette plant est si nuisible. A l'heure actuelle, on croit que la mouche gallicole luttera efficacement contre cette plant nuisible, mais il est encore trop tôt pour évaluer son rendement final.

Introduction

Groundsel bush (*Baccharis halimifolia* L.; Compositae) was introduced into Australia from North America during the last century, probably as an ornamental in Brisbane gardens. By 1900 it was recorded as having escaped from cultivation and had begun to spread (Bailey 1900). It now occurs along the well-watered and productive subtropical lands east of the Great Dividing Range along a coastal strip *c.* 1000 km long by 100 km broad, centred on Brisbane (latitude $27\frac{1}{2}$°) (Fig. 1).

Groundsel bush invades cattle pastures and can quickly form dense woody thickets up to 7 m tall. It is not poisonous to cattle but although young tips are occasionally browsed, stock prefer other pasture. It is undesirable in pasture because it displaces useful fodder plants.

Groundsel bush is a problem for the community rather than just the individual farmer because it produces great numbers of small wind-borne seeds each autumn which can be blown kilometres away. A 2 m high plant may produce half a million seeds (McFadyen 1972). The failure of a landholder to control the weed will inflict a continuing cost on neighbours as they fight a never-ending battle to keep their properties free of groundsel bush from seed blown onto their land.

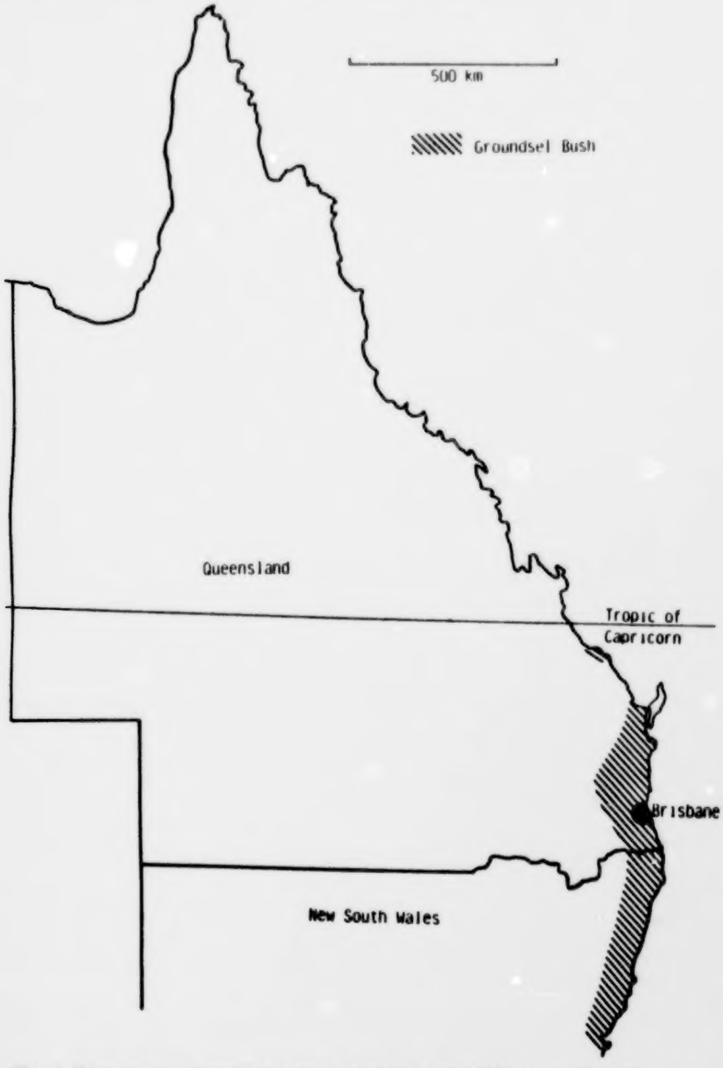


Fig. 1. Distribution of groundsel bush, *Baccharis halimifolia* L., in Australia.

In 1958, Dr. F.D. Bennett of the Commonwealth Institute of Biological Control was commissioned by the Queensland Department of Lands to undertake surveys of organisms attacking *Baccharis* species in North and South America. Between 1967 and 1980 host-specificity investigations were undertaken in Florida, U.S.A, and Parana, Brazil, by Queensland Lands Department entomologists, and more than 20 species of insects were introduced (McFadyen 1979, 1981). One of these was the gall fly *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) which was tested for host specificity by Mr. G. Diatloff of the Queensland Department of Lands in Florida in 1968. In March 1969, in cooperation with Dr. R. Doutt, United States Department of Agriculture, San Francisco, it was introduced into Australia in quarantine, and in May 1969, a small release was made near Deception Bay north of Brisbane. The laboratory population declined rapidly and there were no recoveries following the field release.

In late 1969, further supplies were obtained from Dr. L.A. Andres, USDA, San Francisco, but these died out in quarantine. The lack of success in breeding and field establishment was not encouraging, particularly when compared with the success in the rearing and establishment of other species such as *Trirhabda baccharidis* (Weber) (Coleoptera: Chrysomelidae) and *Aristotelia* sp. (Lepidoptera: Gelechiidae) which were introduced from Florida about the same time and established quickly in Queensland. They were collected off *B. halimifolia* in Florida, an area climatically similar to southern Queensland, whilst *R. californica* was collected off *B. pilularis* DC. from the climatically different San Francisco area (Fig. 2) (Walter and Leith 1960). The failure of the *R. californica* introductions with the possibility of its unsuitability for *B. halimifolia* and Queensland climatic conditions put it low on the priority list for further work. Nevertheless, in June 1982 a further introduction was made from San Francisco, this time into new and much improved heated and humidified quarantine buildings. This time the population increased rapidly and by September 1982 the first releases were made near Brisbane and breeding colonies established in the field by the end of that year.

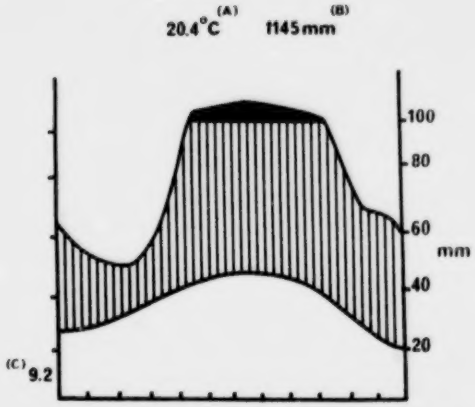
Development of *R. californica* on Groundsel Bush in Australia

R. californica adults are small, delicate flies *c.* 2 mm in length. After they emerge from the gall they mate and lay bunches of red eggs on young growing tips or in leaf axils. The adults rarely live more than a day. The larvae burrow into the tip and a gall, commonly 1 cm but up to 3 cm across, develops within 1 to 2 months (Fig. 3). After the flies emerge from the galls, the gall dies and there is stem dieback usually of 2 cm but up to 10 cm.

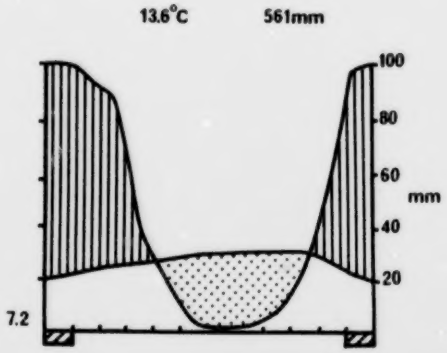
In the U.S.A. the biology and autoecology of *R. californica* on *B. pilularis* has been studied in some detail (e.g. Tilden 1951*a*, *b*; Doutt 1961; Force 1974; Ehler 1979, 1982*a*, *b*). In Australia, its biology and autoecology are generally similar except that the rates of parasitism are lower. Parasitism studies, 18 months after release in Queensland, show rates of parasitism of < 10% (McFadyen, unpubl. data) compared to rates up to 100% in California (Force 1974).

Spread of the gall fly in Australia probably largely depends on it being carried on the prevailing winds. Following a release, galls are commonly found in a 20 m radius around the release point in the first field generation (i.e. *c.* 1 month). However, within 18 months of release at one site, they have been recorded 10 km from the nearest release point and are still spreading.

Most releases have resulted in establishment. Some failures have occurred in late summer at the height of the 1982–83 drought when groundsel bush was drought stressed and not actively growing. Establishment has occurred in a variety of environments; in sun and shade, in coastal, inland and upland regions. In some areas increase has been more rapid than others, but no clear pattern is yet evident. Groundsel bush plants of all sizes are galled from 1 cm high seedlings to the tops of 7 m high bushes.



BRISBANE (45m above sea level)
Queensland



SAN FRANCISCO (16m above sea level)
California

Fig. 2. Climate diagrams (Walter and Leith 1960) of Brisbane and San Francisco: (a) mean annual temperature; (b) mean annual precipitation; (c) mean daily minimum temperature of the coldest month.

Field Assessment of the Effect of R. californica *on Groundsel Bush*

The effect of heavy galling on flowering and seeding was assessed by comparing a heavily galled release site with similar sites nearby where galling was still low. The comparisons were made by aerial photography and by sampling plants. The area chosen for these comparisons was about 50 km south of Brisbane in the catchment area of the Hinze Dam (*c.* 20°S latitude). It is an area of wooded hills interlaced with ravines from which water intermittently flows into the Nerang River and then to the Hinze Dam. The river flats and some of the hillsides had been originally cleared for grazing and agriculture and are now densely covered with groundsel bush. On 12 November 1982, a release of eight pot plants of groundsel bush infested with galls of *R. californica* was made amongst a pure stand of 5 m high groundsel bush on alluvial river flats (Whipbird site).

Aerial Photographs

The purpose of the aerial photographs was to show the lack of flowers in galled areas and the abundance of flowers in ungalled areas. On 27 April 1984, aerial photographs were taken after flowering (when female plants are a dense mass of white and thus easy to see). The white appearance of the female plant is due to the expansion of the white parachute-like pappus attached to the seed. For a period of about 2 wks, the plants are a showy spectacular sight.

Fig. 4 is an aerial photograph of the general area taken at *c.* 1500 m. The reduction in flowering can be seen as marked. Figs. 5 and 6 are sections of the same area taken at *c.* 300 m. Fig. 5 is the heavily galled release area (Whipbird site) of *c.* 1 ha showing very little seed. Fig. 6 is a relatively lightly galled area and the white female plants are clearly evident.

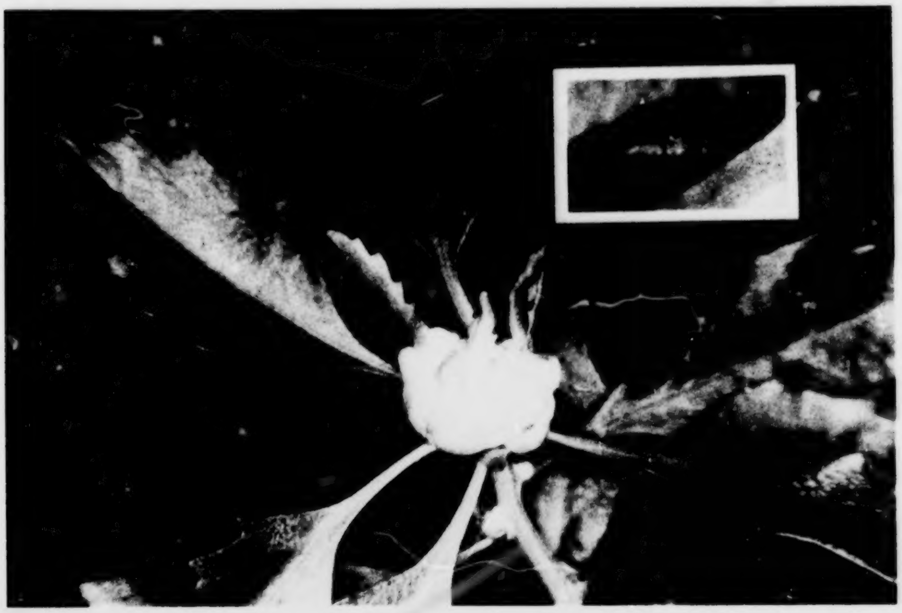


Fig. 3. *Rhopalomyia californica* Felt gall on groundsel bush, *Baccharis halimifolia* L. Inset: female *R. californica*.

Sampling Trials

Two sites were chosen 3 km apart. Both were on flat land fronting the Nerang River pondage of the Hinze Dam. In both areas, the groundsel bush was a pure stand *c.* 5 m tall. At the release site (Whipbird site), plants were heavily galled; at the control site (Boat site), only the occasional plant had a gall. One tip gall on a 5 m high bush with hundreds of ungalled tips was considered negligible damage by the gall fly, so the Boat site was regarded as being unaffected by the gall fly.

The sampling method at the Whipbird and Boat infestations was to select randomly 30 quadrats of 0.25 m^2 (0.5 × 0.5 m) and place four poles at each corner of the quadrat. This formed a column up through the groundsel bush. All flower buds falling within this column were collected and counted. All quadrats were under full groundsel bush canopy.

The results presented in Table 1 show a very considerable average reduction of 93% in the number of capitula produced. It is clear from both the ground sampling and the aerial photography that the gall fly has caused a major reduction in seeding.

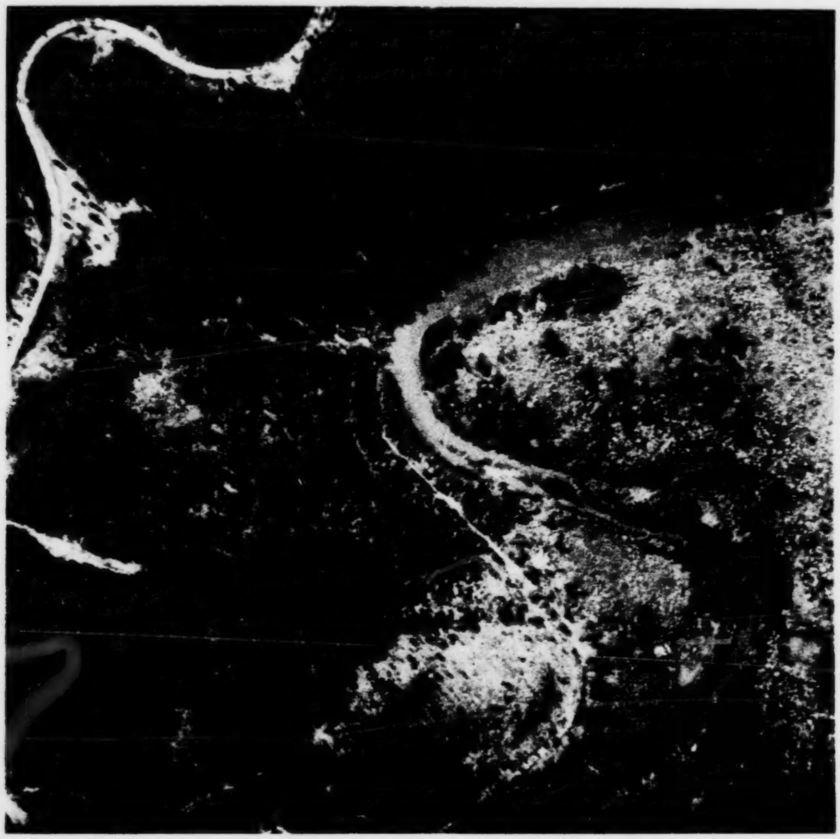


Fig. 4. (A) points to the release area of heavily galled, 5 m high groundsel bush, *Baccharis halimifolia* L. (B) points to white flowering female groundsel bush plants unaffected by gall fly, *Rhopalomyia californica* Felt.

Discussion

As *R. californica* was released less than 2 yrs ago, it is too early to know if it will be equally effective in all areas or whether some factor such as a sudden increase in parasitism may render it ineffective. However, it continues to increase and spread and as each month goes by, the confidence in its usefulness increases. Providing this increase and spread continues, it will cause a considerable reduction in the amount of seed produced.

As most seed falls quite close to the parent plant (Diatloff 1964), intraspecific competition among seedlings is important here, but not for seedlings from seed blown to clean or sparsely infested areas. In the latter case, any reduction in the total amount of seed produced will mean a reduction in the spread of the weed as there will be fewer seedlings infesting clean areas. Additionally, attack by the gall fly on seedlings could be expected to slow seedling growth and increase seedling mortality rates, thereby further reducing the rate of spread. In the long term, the gall fly may kill mature plants by depleting their food reserves, but this remains to be seen. No clear evidence of plant death due to galling has been seen in the field so far, other than a few seedlings where galling is likely to have been a contributing factor.

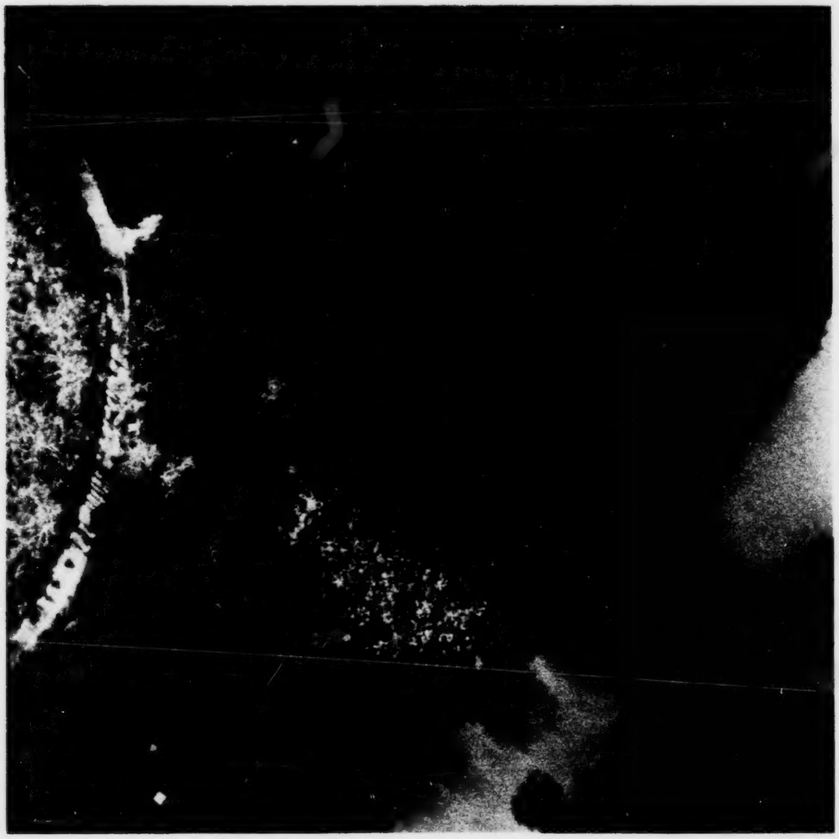


Fig. 5. *Rhopalomyia californica* Felt release site (Whipbird site) with heavy gall fly attack. Few plants are flowering.

Apart from the practical advantages of the control of groundsel bush, the success of the gall fly in Australia illustrates some of the difficultues of prediction in biological control. It seems reasonable to assume that an insect from a similar climate and from the same plant species will be a more successful biocontrol agent than one from a different climate and from another plant species, albeit closely related. In the biocontrol programme against groundsel bush, insects which appeared the most logical choice were tried without success, whilst an insect which appeared to have only an outside chance in comparison so far appears to be successful. The difficulties of accurate and reliable prediction are obviously considerable.

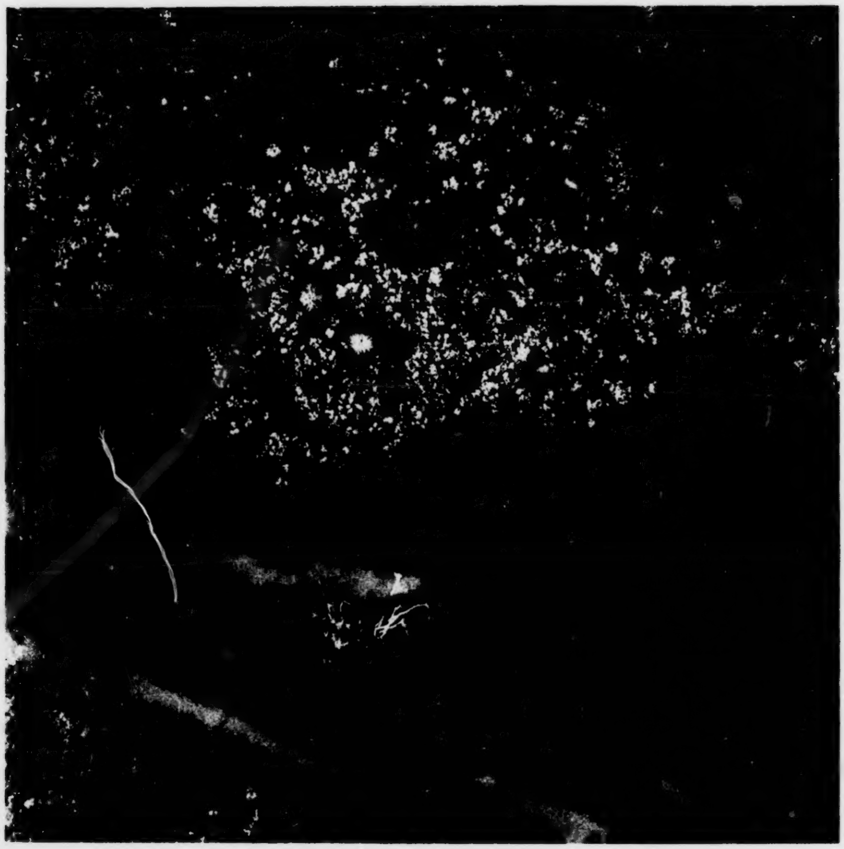


Fig. 6. An area only lightly attacked by *Rhopalomyia californica* Felt. Many white flowering female groundsel bush (*Baccharis halimifolia* L.) plants are evident.

Table 1. Effect of the gall fly *Rhopalomyia californica* Felt on seeding by groundsel bush (*Baccharis halimifolia* L.)

Site	Mean no. of flower heads per sample	Range	Percent reduction in seeding
Whipbird site (galled plants)	220	0-1,401	93%
Boat site (ungalled plants)	3,114	446-11,225	0%

Acknowledgments

Mrs. N. Riding, Miss M. Ablin, Mr. M. Trevino, Mr. T. Ellis and many other staff of the Alan Fletcher Research Station reared, distributed and assisted in the sampling of the gall fly, and Mr. Myint Thaung of the University of Queensland and Mr. A. Vuocolo of the Queensland Institute of Technology sampled for parasitism. Their hard and dedicated work is most gratefully acknowledged. I also wish to thank Messrs. A. Betts and A. Eccles, Queensland Department of Forestry who kindly arranged and undertook the aerial photography and Mr. D. Paetzholdt, Queensland Department of Mapping and Surveying, for his helpful advice about the aerial photography.

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The Biological Control Programme Against *Parthenium hysterophorus* in Queensland

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Abstract

Between 1979 and 1983 seven species of insects were imported from Brazil and Mexico for the biological control of *Parthenium hysterophorus* (Compositae) in Queensland. Detailed testing on six of these showed them to be host-specific and field releases were made between 1980 and 1984. So far, three species have established: a stem-boring weevil, *Listronotus setosipennis* (Coleoptera: Curculionidae); a leaf-feeding chrysomelid, *Zygogramma bicolorata* (Coleoptera: Chrysomelidae); and a stem-galling moth, *Epiblema strenuana* (Lepidoptera: Tortricidae), but only the last is having any impact on the weed. In the 18 months since initial release, this moth has increased and spread dramatically, and there are excellent prospects for substantial biological control of parthenium weed. The closely related weeds *Ambrosia artemisiifolia* (Compositae) and *Xanthium strumarium* (Compositae) are also attacked, and substantial control of these may also be achieved. The implications of the use of insects capable of attacking several related weeds are discussed.

Programme de Lutte Biologique Contre *Parthenium hysterophorus* à Queensland

Dans le cadre d'un programme de lutte biologique contre *Parthenium hysterophorus* (Composée) à Queensland, sept espèces d'insectes ont été importées du Brésil et du Mexique entre 1979 et 1983. D'après les essais exhaustifs, six espèces n'adoptent qu'un unique hôte, et des lâchers sur le terrain ont été effectués entre 1980 et 1984. Jusqu'à présent, trois espèces se sont établies, à savoir un charançon perce-tiges *Listronotus setosipennis* (Coleoptera: Curculionidae), une chrysomèle se nourrissant de feuilles *Zygogramma bicolorata* (Coleoptera: Chrysomelidae) et un lépidoptère provoquant la gale des tiges *Epiblema strenuana* (Lepidoptera: Tortricidae), mais seule la dernière espèce influe de façon notable sur la plante nuisible. Au cours des 18 mois qui se sont écoulés depuis l'introduction initiale, les populations de lépidoptères ont augmenté et se sont disséminées de façon marquée, et cet insecte semble être très prometteur pour la lutte biologique contre la plant nuisible *Parthenium*. Le lépidoptère s'attaque également aux plantes nuisibles étroitement apparentées *Ambrosia artemisiifolia* (Composée) et *Xanthium strumarium* (Composée), contre lesquelles il constituera sans doute un excellent agent biologique. Le rapport traite des conséquences de l'utilisation d'insectes pouvant s'attaquer à plusieurs plantes nuisibles de la même famille.

Introduction

Parthenium weed, *Parthenium hysterophorus* L. (Compositae), an annual herb native to the neotropics, has become a serious weed in many parts of the world (Towers *et al.* 1977). It was first collected in Australia in 1955 from the upper Brisbane valley in Queensland but in 1964 was recorded from the Central Highlands of this State where it was established from contaminated grass seed imported from Texas (S. Everist, unpubl. rept, 1976). The weed spread rapidly and now infests thousands of square kilometres in Queensland (Auld *et al.* 1983). It is still spreading with over 100 small infestations recently reported in New South Wales.

In 1975 parthenium weed was declared a noxious weed in Queensland and in 1976 a programme of biological control was initiated at the same time as a containment scheme to control spread to new areas (Haseler 1976). An entomologist from the Alan Fletcher Research Station went to south-west Brazil from 1977–81, and from 1978–83 the Commonwealth Institute of Biological Control was contracted by the Queensland Department of Lands to investigate possible biological control agents in Mexico (McClay 1985).

Insects Introduced

Only preliminary host testing was carried out in both Brazil and Mexico, against 9 to 10 plants in the tribe Heliantheae of the Compositae, with particular emphasis on sunflower (*Helianthus annuus* L.) and guayule (*Parthenium argentatum* Gray), two closely related plants of economic importance. Suitable species were then sent to Queensland for detailed testing in quarantine against a list of about 50 economic plants in 27 families (McFadyen and McClay 1981). Between 1979–80, seven species were imported into quarantine. A root-feeding weevil, *Thecesternus hirsutus* Pierce (Coleoptera: Curculionidae), was not successfully reared in quarantine and host testing was never completed; the other six species proved sufficiently host specific and were subsequently field released. The seed-feeding weevil, *Smicronyx lutulentus* Dietz (Coleoptera: Curculionidae), was released between 1980–83 but failed to establish. The sap-sucking bug *Stobaera concinna* (Stål) (Hemiptera: Delphacidae) and the leaf-mining moth *Bucculatrix* sp. D (Lepidoptera: Lyonetiidae) were first released in September 1983 and January 1984, respectively, and establishment has not been confirmed. The remaining three species have established. *Listronotus setosipennis* (Hustache) (Coleoptera: Curculionidae), a stem-feeding weevil from Brazil which has been released since January 1983, appears to have established; however, the population levels in the field are very low and the impact on the plant negligible. *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae), a leaf-feeding beetle released from December 1980 to May 1983 (McFadyen and McClay 1981), has established in some areas but appears to be restricted by poor survival if rain is delayed till late in the year, as is common in central Queensland.

The Stem-galling Moth *Epiblema strenuana* (Walker) (Lepidoptera: Tortricidae)

The only species to have reached damaging numbers is *E. strenuana*. The biology of this moth is described by McClay (*in press*). Eggs are laid singly on the underside of leaves, and larvae bore into stem tips or axillary buds. The plant swells to form a fusiform gall, inside which the larva feeds until full size, about 10 mm long. Pupation occurs in the gall and the adult emerges through a thin-walled 'window' cut by the larva. In summer, the life cycle from egg to adult is about 5 wks and moths in the laboratory in Queensland lay up to 250 eggs each. *E. strenuana* is widely distributed throughout North America where it is recorded from *Ambrosia trifida* L., *A. artemisiifolia* L., *A. psilostachya* DC. (Compositae), *P. hysterophorus*, and *Xanthium commune* Britton (Compositae) (McClay, *in press*).

Establishment and Spread

The first field releases of *E. strenuana* were made in December 1982, and by February 1984 a total of 35,000 pupae had been released at 36 sites, mainly in the central highlands of Queensland, where the largest infestations of parthenium weed occur.

Initially, conditions were very dry in this normally summer-rainfall area, until in April–May 1983 there was widespread heavy rain with resulting germination of parthenium weed. Most areas then experienced an exceptionally wet, mild winter and spring, and sufficient summer rain for continued growth of parthenium weed. Of the earlier releases, three established well from the outset, with large populations present by August 1983 (spring). By January 1984, at these three sites there were 500–800 galls m^{-2} over several ha of dense parthenium and collection and distribution of field material began soon after. By May 1984, the moth was present over most of the 120,000 km^2 affected by parthenium weed, and had reached damaging levels over at least 25% of this area. Travelling with the prevailing winds, in 12 months the moth in one place was present 160 km from the nearest release, crossing a low range of hills en route.

This phenomenal increase was aided by two factors: first, the very favourable weather conditions from April 1983 on; and second, the fact that the moth also attacks Noogoora burr, *Xanthium strumarium* L., which is a widespread weed over most of the State. In many instances, *E. strenuana* has spread on Noogoora burr into areas where parthenium weed occurs only as isolated patches. Furthermore, although Noogoora burr is also an annual, in central Queensland it tends to germinate longer after rain than does parthenium weed, and to remain green much later. Thus the moth has continued to increase in Noogoora burr at times when no suitable parthenium weed was present.

Mortality Factors

One of the most striking features of the increase of *E. strenuana* in Queensland has been the almost total absence of mortality in larvae and pupae. Mortality in adults and eggs has not been estimated, but must be very low in favourable conditions with abundant suitable plants, as increases of nearly 100 fold in each generation have been observed. Presumably if adults have to search over long distances for suitable plants, adult mortality would be substantial. Among small larvae, the only significant cause of mortality is drought stress in the plants. Females will only lay on plants in good condition, but if severe wilting occurs over the next 2–4 wks, which is not uncommon in summer, many small larvae die *in situ* or after leaving the wilted plant.

In large larvae and pupae, there is virtually no mortality. Predation is extremely rare, as the gall is closed. Large larvae usually survive water stress in the plant, sometimes feeding down into the stem where they successfully complete development. If plants die from other causes, such as excessive numbers of galls, larvae will leave galls and transfer successfully to adjacent plants. In the field this is quite common at high population levels, in contrast to the situation in Mexico (McClay, *in press*).

Parasitism is also very low, in contrast to the Americas (McClay, *in press*). Five parasites have been recorded: *Bracon* sp. (Hymenoptera: Braconidae); *Apanteles* sp. (Hymenoptera: Braconidae); an undetermined species (Hymenoptera: Eupelmidae) from the larvae; *Glabridorsum* sp. (Hymenoptera: Ichneumonidae); and *Antrocephalus* sp. (Hymenoptera: Chalcididae) from the pupae. The greatest total parasitism so far recorded was 10% at Sherwood, Brisbane, in February 1984. In the Central Highlands, an ecologically less-diverse region, no parasites have yet been found.

Phenology

In McClay (*in press*) it is clear that in Mexico the population is strongly seasonal, overwintering as pre-pupal larvae from October to February inclusive. In Queensland, overwintering appears to be more flexible. Readiness to enter pre-pupal diapause must be initiated by shortening daylength, as diapause does not occur in summer. However even after the autumn equinox (March in Australia), diapause requires the additional stimulus of either low temperatures (minima below about 10°C) or senescence of the plant. Thus in Brisbane in 1984 pupation continued until early May when, following a cold period of several days, pupation ceased. In central Queensland, where temperatures were still very high at the end of May, pupae were present as long as the plants were actively growing; i.e. where moisture was available. In senescing plants, only diapausing pre-pupal larvae, but no pupae, were found in April and May.

This flexibility is ideally suited to conditions in central Queensland, where a prominent feature of the climate is extreme variability from year-to-year. In general, winters are cool and dry, with frosts in June and July. However, in some years high temperatures persist well into June, frosts are almost absent, and rainfall is sufficient to maintain plant growth throughout. Thus in many areas *E. strenuana* was able to breed continuously from early August 1983 to the end of May 1984, probably passing through seven or eight generations. There was no evidence of separate generations after the first spring generation (moths emerged and laid eggs end of August, pupae abundant middle of October).

Damage Caused

E. strenuana attacks plants of all sizes from rosette to mature, if green leaves are present. A single gall on a small rosette plant may prevent all further growth, or even kill the plant. On larger plants, damage depends on the number of galls present, and 5–10 galls in a large plant effectively prevents seed production. In the best field sites, an average of 5–10 galls/large plant (2 galls/plant including seedlings, 400–800 galls m^{-2}) was reached by January 1984 and maintained since. Over several ha at these sites very little seed was produced, parthenium stands were reduced from 150–200 cm to only 20–30 cm high, and there was a very noticeable increase in grass production. By May 1984, a similar level of attack on the few plants still actively growing was present over large areas, perhaps a quarter of the approximately 120,000 km^2 involved. Over much of the rest of this area, galls were present at levels varying from 1 gall/large plant (40 galls m^{-2} in dense parthenium) to 1 gall/20 plants. At this level, the effect is negligible; however if favourable conditions continue the population could increase 10–100 fold in one generation.

Attack on Other Plants

Both the known host range in the Americas and the results of laboratory tests showed that *Ambrosia* and *Xanthium* species were likely to be attacked. As these genera are present in Australia only as introduced, declared-noxious weeds, subject to control measures wherever they occur, this was regarded as beneficial rather than otherwise. *X. strumarium* occurs throughout Queensland as scattered plants in moist places, becoming more abundant in the west when rainfall is adequate. *X. spinosum* L. is also widespread but less common (Kleinschmidt and Johnson 1977) and both also occur widely in New South Wales. *A. artemisiifolia* is confined to the southeast corner of Queensland (Fig. 1) where, however, it is increasing rapidly (McFadyen 1984). *A. psilostachya* and *A. (Franseria) confertiflora* DC. occur only as very limited infestations, though the former is more common in New South Wales (Whittet 1968).

Attack on *X. strumarium* and *X. spinosum* by *E. strenuana* was first observed in January 1984. *X. spinosum* is not common in central Queensland where the first releases were made, and although some galls were found, there seems to be little attack on this species. *X. strumarium* is common throughout along creeks and riversides, in low-lying areas after flooding, and around waterholes and dams. By May 1984, *E. strenuana* galls were present in most patches of plants over at least 60,000 km^2. In most of this area the density was low, 1–5 galls/large plant, at which level damage is minimal. However in some localities over 50% of seedling plants were heavily galled.

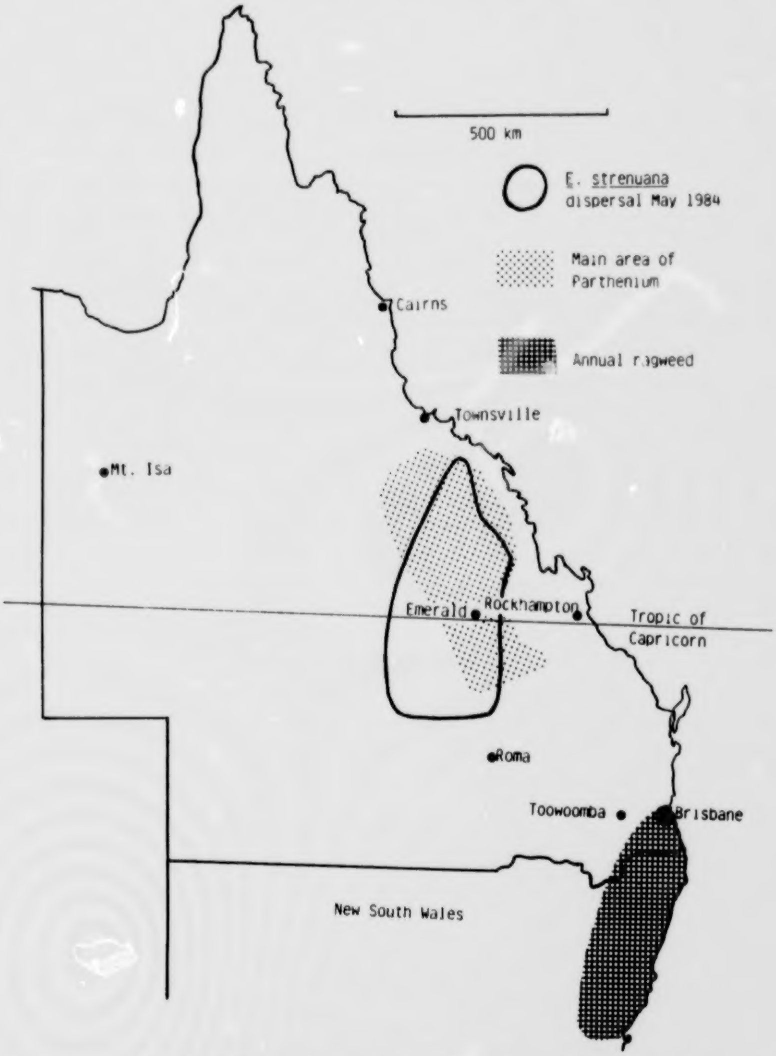
500 km
E. strenuana dispersal May 1984
Main area of Parthenium
Annual ragweed
Cairns
Townsville
Mt. Isa
Emerald
Rockhampton
Tropic of Capricorn
Roma
Toowoomba
Brisbane
New South Wales

Fig. 1. Distribution of parthenium (*Parthenium hysterophorus* L.) and annual ragweed (*Ambrosia artemisiifolia* L.) in Queensland.

Field attack on *A. artemisiifolia* was first observed in Sherwood in January 1984, and in February and March releases were made on this species south of Brisbane. The moth has established, but the population is still low, and further increase and spread will be delayed until spring (August–September 1984).

Future Prospects

After field releases over 18 months, *E. strenuana* is already present in most of the 120,000 km^2 affected by *P. hysterophorus* (Fig. 1), and further distribution will only be necessary in some isolated areas, or where very dry weather in 1983–84 limited increase. The degree of control obtained in the 1984–85 summer will depend entirely on rainfall, as *E. strenuana* will probably be less successful in dry conditions, even though a reasonable population persists on plants occurring in moist situations. Indeed, initial establishment and spread took place in January–April 1983 at the end of a severe 3-yr drought. Increase to damaging levels nevertheless probably needs widespread rain. However, as drought conditions also restrict seed production in these annual weeds, it now appears likely that adequate control of *P. hysterophorus* will be obtained in the long term. As *P. hysterophorus* is not poisonous, it is only a problem because at high densities and producing enormous quantities of seed, it is an aggressive invasive weed of pasture and crops. If restricted to small areas along creeks, in cattle yards, etc., *P. hysterophorus* would no longer be a problem. Whether this degree of control is reached in 3–5 yrs, or 10–15 yrs, depends in my opinion entirely on the climate, with *E. strenuana* favoured by wet years. Heavy rain in eastern Australia in late July 1984 should ensure favourable conditions this spring.

Control of *X. strumarium* is more problematical for two reasons. First, in central Queensland *X. strumarium* is already fairly well-controlled by the rust *Puccinia xanthii* Schw. (Uredinales) (Julien *et al.* 1979), and only occurs as relatively small patches. It is a problem even at this low density because the seedlings are poisonous to livestock (Everist 1974), and the burrs become entangled in wool, lowering its value. Second, in the west where the rust is ineffective and *X. strumarium* is still common, rainfall is both lower and more unreliable, so that *E. strenuana* could be expected to be less effective. However, overall *E. strenuana* attack must reduce vigour of this species to some extent, and further releases are planned for summer 1984–85 in western Queensland and northern New South Wales where *X. strumarium* is a problem.

The prospects for biological control of *A. artemisiifolia* are much better. The only factor limiting *E. strenuana* in Queensland seems to be drought, and along the coast where this weed occurs, rainfall is both higher and more reliable. As the first releases here were only made in February and March 1984, it is still too early for results, but I would confidently expect these to be excellent. The only possible problem would be parasitism, as five parasite species have been recorded in the coastal region. However parasitism has remained very low, even at Sherwood where galls have been present in outside cages for 18 months. Releases of *E. strenuana* are planned for summer 1984–85 in ragweed areas in southeast Queensland and northern and central New South Wales.

Discussion

E. strenuana is an insect that has been known for a long time, having been recorded on *X. strumarium* in the 1930s by Australian entomologists looking for biocontrol agents in the U.S.A. In eastern America, it is common and sometimes damaging on *Ambrosia* spp. (Stegmaier 1971). Nevertheless it was never considered as a potential biocontrol agent, because its host range of *Ambrosia*, *Xanthium* and *Parthenium* was considered unacceptably wide (Hilgendorf and Goeden 1983; Goeden, pers. comm., 1984).

These three genera are currently in the tribe Heliantheae of the family Compositae. In previous classifications based on floral structures, *Parthenium* was placed in the sub-tribe Melampodiinae, while *Ambrosia* and *Xanthium* were in the sub-tribe Ambrosiinae. However Stuessy (1973) included *Parthenium* in the Ambrosiinae, based on chromosome numbers, leaf type, and particularly on presence in the plants of similar complex sesquiterpene lactones. In the tribe Heliantheae (*sensu* Stuessy) these lactones are found in only four of the 15 sub-tribes. Most species in all eight genera in the sub-tribe Ambrosiinae (*sensu* Stuessy) contain these lcatones, while in the other three sub-tribes they only occur in some genera. Within the Ambrosiinae, the highly characteristic class III and class IV lactones (ambrosanolides) occur in *Ambrosia*, *Parthenium*, and *Hymenoclea*, while xanthanolides occur in *Xanthium* and *Parthenice*, and both types are found in *Iva* (Hertz 1977).

It is thus clear that the three genera *Parthenium*, *Ambrosia* and *Xanthium* are very closely related, and this grouping of *Parthenium* with *Ambrosia* is in agreement with the host range of many *Parthenium* insects. Recent studies have shown that there is a close affinity between the insects attacking *Ambrosia* spp. and those of *P. hysterophorus* (Gagné 1975; McClay 1983). Furthermore *E. strenuana* belongs to a genus of very host-specific root- and stem-galling moths, with hosts entirely in the Compositae, which suggests a long evolutionary relationship between insect and host. *E. strenuana* occurs throughout much of North America, including large agricultural areas with a wide variety of crops. Agricultural entomology in the U.S.A. is highly developed and any attack by *E. strenuana* or other *Epiblema* spp. on sunflower or other crops would have been recorded. It can thus be unwise to rely too heavily on the systematic position of plant genera, when considering insects as potential biological control agents. Systematics change, and some botanical families have not been revised for a very long time.

The other side of the coin, of course, is that *E. strenuana* is likely to attack most plants in these three genera. In Australia there are no native plants in the sub-tribe Ambrosiinae nor closely related to them, and the only representatives occurring in the country are introduced species, most of which are serious weeds. The only plant with possible economic value is guayule, *P. argentatum*, and this is not attacked by *E. strenuana* either in tests or the field (McClay, *in press*). *P. argentatum* lacks the characteristic sesquiterpene lactones (Swain and Williams 1977) and supports a very different insect complex. Consequently, Australian Plant Quarantine authorities permitted the introduction and release of *E. strenuana*, and general opinion in the country is that if the moth succeeds in significant control of *Xanthium*, *Ambrosia*, and *Parthenium*, it will be hailed as a supermoth and saviour!

In other countries the situation may be different. Biological control of *P. hysterophorus* and of *Ambrosia* spp. is being pursued by India and the USSR. These countries have native species of *Xanthium* which *E. strenuana* might well attack and this would have to be taken into account. However, *E. strenuana* is the most promising of the biological control agents currently being tried for weeds in these genera, and its introduction should be seriously considered wherever native species are not at risk.

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A Most Promising Bud-galling Wasp, *Trichilogaster acaciaelongifoliae* (Pteromalidae), Established Against *Acacia longifolia* in South Africa

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Abstract

Trichilogaster acaciaelongifoliae is one of many specialized natural enemies that suppress seed production by *Acacia longifolia* in Australia, and it was recently (1981) released against this weed in South Africa. Adults live for a few days, larvae gall buds, and the species is univoltine. The incidence of males in colonies from different sources in Australia may vary from rare to abundant, depending on the source. Damage by *T. acacialongifoliae* in Australia is infrequent and unimpressive because of high levels of parasitism. Surveys in Australia, and specificity tests in South Africa showed that the wasp is restricted to *A. longifolia* and *A. floribunda*. Once suitable collecting and shipping techniques were developed, establishment was easy and rapid. Observations at a few urban sites in Australia where this insect was found largely isolated from its parasitoids, and at release sites in South Africa indicated that it may be much more destructive to the host than would be anticipated from an agent acting primarily on inflorescence buds.

Evaluations at two release sites have shown that both seed production and vegetative growth of the weed are markedly reduced by galling.

Une Guêpe Qui Provoque la Gale des Bourgeons, *Trichilogaster acaciaelongifoliae* (Pteromalidae), Agent Efficace de Lutte Biologique Contre l'Arbuste Ligneux *Acacia longifolia* en Afrique du Sud

Trichilogaster acaciaelongifoliae est l'un des nombreux ennemis naturels spécialisés qui empêchent la formation des graines de *Acacia longifolia* en Australie, et cet insecte a récemment (1981) été introduit en Afrique du Sud pour lutter contre cette plante nuisible. Les adultes vivent quelques jours, les larves provoquent la gale des bourgeons et l'espèce est univoltine. Les mâles sont habituellement rares et peut-être inutiles. Les dommages causés par *T. acaciaelongifoliae* en Australie sont peu fréquents et négligeables en raison de hauts niveaux de parasitisme. D'après des études menées en Australie et des assais de spécificité effectués en Afrique du Sud, cette guêpe se limite aux plantes hôtes *A. longifolia* et *A. floribunda*. Dès que des techniques appropriées pour recueillir et transporter les insectes ont été mises au point, le'établissement a été facile et rapide. Les évaluations ont mis en évidence que, outre l'élimination quasi totale des graines, les insectes ont réduit de façon considérable la croissance et la vigueur des plantes, même lorsque le nombre de gales était limité. Ces résultats infirment les prévisions théoriques selon lesquelles les insectes galligènes constituent des agents biologiques inefficaces.

Introduction

Acacia longifolia (Andr.) Willd. (Leguminosae), a woody, perennial shrub to small tree from southeastern Australia has become naturalized in the southwestern and southeastern Cape where it is a serious and troublesome weed along watercourses and in valleys and on mountain slopes with deeper soils. It invades and replaces natural vegetation, forms dense thickets (Boucher and Stirton 1978), and affects normal water flow along streams. Control is expensive and difficult, perhaps largely because of the copious production of long-lived seeds accumulating in the soil, stimulated to germinate and to form dense stands after fires (Fig. 1) and constantly germinating next to watercourses after floods.

In its natural distribution in eastern Australia the plant is attacked by a variety of insects. Van den Berg (1982*a, b, c*) reported on stem- and root-borers, sap-suckers, leaf-miners, defoliators, and species developing in pods and seeds.

A subsequent study (unpubl.) revealed further natural enemies that may be useful in defoliating the plant; e.g. an apparently undescribed species of the genus *Rayieria* Odhiambo (Hemiptera: Miridae), and others that may suppress flowering and seeding, such as an eriophyid mite in young inflorescences, an unidentified cosmopterigid peduncle-boring larva, cecidomyiids developing in unopened florets (provisionally identified as *Asphondylia* sp. 1), in newly set podlets (?*Dasineura* sp.) (cf. '*Cecidomyia*' *acaciaelongifoliae* described by Skuse 1890) and in young pods (*Asphondylia* sp. 2) and an unidentified *Bruchophagus* sp. (Hymenoptera: Eurytomidae) developing in immature seeds.

The brachyscelidiphagine gall-wasp *Trichilogaster acaciaelongifoliae* (Froggatt) (Hymenoptera: Pteromalidae) described from *A. longifolia* in New South Wales (Froggatt 1892) and from Queensland (Girault 1913), was one of the several species recommended for further studies (Van den Berg 1977) and after specificity studies (Van den Berg 1980; Neser, unpubl. data) were completed, the first small releases were made in December 1981 (Dennill 1985).

The very short-lived females (most die within 2–3 days) emerge from the galls on a particular plant over a brief period (1–2 wks) in summer and immediately lay eggs (Fig. 2) in young axillary buds destined to develop into inflorescences during the following 8–10 months. At the time shortly before, during, and soon after flowering, the affected buds enlarge rapidly, to form round, single-celled, to larger, irregular, multicelled galls (Fig. 3), the contained larvae (Fig. 4) mature and pupate and the new generation of adults appear in November to January when the next season's inflorescence buds are present on the plant. The biology of the insect on its only three known hosts, now regarded as two varieties of *A. longifolia* (the typical variety, and var. *sophorae* [Labill.] F. Muell.) and *A. floribunda* (Vent.) Willd. (see Costermans 1981: 304–5) was carefully studied and reported by Noble (1940). Somewhat puzzling features he mentioned were the virtual to complete absence of males in populations on *A. longifolia* and the presence of about 50% of males in batches reared from *A. floribunda* (Noble 1940: 23). He also commented on the extreme patchiness of populations of the wasp: often only single plants in a group would be heavily galled with no galls on adjacent plants. Van den Berg (pers. comm., 1976) also noticed a very sparse and patchy occurrence of galls on *A. longifolia* in southeastern Australia. Noble (1940: 22) ascribed the phenomenon to poor powers of flight and the fact that the newly emerged females tended to lay eggs on the immediate vicinity of the galls from which they had emerged. He, however, also mentioned (p. 32) that the degree of parasitism and composition of associated and parasitoid species varied markedly between different plants in the same area.

Results and Discussion

During collecting trips in New South Wales, Victoria and Tasmania during the summers of 1981 and 1982 to obtain large numbers of pupae of the wasp for shipment to South Africa, it was found that the proportion of larvae and pupae parasitized by mainly the two species of *Megastigmus* (Hymenoptera: Torymidae) and two *Eurytoma* spp. (Hymenoptera: Eurytomidae), or outcompeted by larvae of mainly *Acrocercops eumetalla* (Meyrick) (Lepidoptera: Gracillariidae) (most likely the species referred to by Noble 1940), was generally very high (70–90% and occasionally and locally approaching 100%). This was seen as part of the reason why heavily galled plants were so rare and why populations of the wasp appeared to be so localized: populations were probably founded by occasional females that dispersed into areas where the new colonies flourished until reached by the parasitoids, which then reduced the gall wasp populations to the generally observed very low levels. Parasitoids and secondary insects developing in the galls are therefore seen as the reasons why *T. acaciaelongifoliae* overall does not appear to be an important natural enemy of *A. longifolia* in Australia.

A shipment of about 1000 galls from *A. longifolia* collected near Melbourne in November 1980 and shipped to South Africa yielded only four weakened *T. acaciaelongifoliae* females and numerous parasitoids. Despite efforts to keep the galls as long as possible to allow maximal emergence, most of them decomposed. This illustrates some serious early problems experienced in shipping large numbers of this insect to South Africa: (1) once collected, the very succulent galls deteriorate and rot rapidly in humid conditions, and dehydrate quickly in drier conditions — both situations rendering the galls unsuitable for emergence by the short-lived, delicate adult females; (2) the galls should be collected and shipped only during the last 7–10 days before the adults emerge, to prevent massive mortality in transit and/or emergence of weakened wasps; and (3) because reliance had to be placed on field-collected rather than laboratory-reared specimens, sources relatively free from parasitoids had to be found.

For the large shipments planned for 1981–82, various possible collecting sites were visited and samples of galls from each were dissected from time to time to note degree of parasitism and developmental stage of larvae. This allowed early location of suitable collecting sites (or of individual suitable plants) and an estimated best collecting date for each site, group of plants in a general area, or even for individual selected plants. The periods of peak emergence of wasps in different parts of coastal and near-coastal southeastern Australia occurred from about mid-October to late January. For instance, near the coast between Newcastle and Gosford (50–120 km NNE of Sydney), peak emergence in 1981 and 1982 occurred during the last 2 wks of October; in and around Sydney (± 34°S, 151°E) it was about a week later (late October to early November); around Jervis Bay (140 km SSW of Sydney), it was around mid-November; and between Mittagong and Fitzroy Falls (about 100 km SW of Sydney and 40 km inland from the coast) it was a week later. Further southwest, in and around Melbourne (± 38°S, 145°E) peak emergence was expected to occur about mid-December 1982, and at Launceston (± 41°30′S, 147°E) in Tasmania emergence had not started by early January 1981 and was expected to occur in the second half of January. The growing cycle and maturation of inflorescences probably determine onset of rapid growth of larvae in galls, and emergence in an area (or at any particular site or during a particular year), may be closely tied to flowering time and prevailing growing conditions for the host plant.

For shipments it was endeavoured to collect the galls when about 10–15% of adults had emerged, which ensured that the majority of the remainder would emerge in the following week or two, before the galls deteriorated.

Parasitism was generally found to be much lower in galls on plants in towns and cities, compared to plants in relatively undisturbed situations. Thus *A. longifolia* planted in gardens and next to streets in urban areas (e.g. Sydney; the coastal town Moruya,

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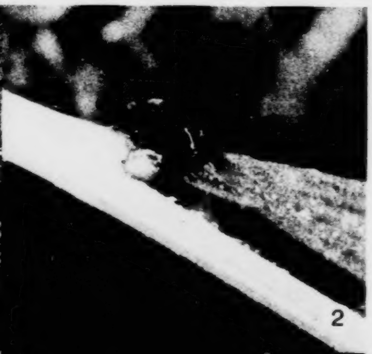
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New South Wales; an industrial area in Geelong, Victoria; a bitumin-sealed parking area in Launceston, Tasmania; metropolitan Melbourne, where the plants were sooty from pollutants in the air; or some planted next to some major freeways), were found to be the best sources of largely unparasitized pupae for shipment to South Africa.

The first 265 females were released on 31 sleeved *A. longifolia* branches at two sites near Stellenbosch and the gauze sleeves were removed a week later (Dennill, 1985). Even with the high stocking rates (in hindsight) of 5–10 females/branch, establishment at these sites was readily accomplished, as shown by the effect of galling that occurred in the 2 yrs after the wasps were allowed to spread (Dennill 1985).

Larger releases (made by simply releasing females, newly emerged in quarantine from surface-sterilized galls shipped from Australia) were made possible by exploiting the collecting strategies outlined above. In November–December 1982, 14,800 females were released at several sites in the southwestern Cape, and in December 1983, galls were so abundant at the release sites that redistribution to 64 additional sites was possible. Establishment has also been achieved from an initial small release in December 1982 of a few females at Grahamstown in the eastern Cape, where further releases were made in 1983.

Where *A. longifolia* was heavily galled in urban sites in Australia (where parasitoids did not have the usual suppressing action on the gall wasp populations), it was possible to get an idea of the possible effect that this insect might have in South Africa. It was noticed that pods were absent on galled branches, which also displayed paucity of new side shoots (the following year's fruiting branches), and even die-back of the terminal growth. At one site (urban Geelong) galling was so heavy that many of the plants, further stressed by drought in November 1982, dropped most of their phyllodes (Fig. 5) and on particularly badly affected branches the galls were only a fraction of their normal size (Fig. 6) and contained only small insects, instead of the fully developed larvae and pupae which would be expected there in November. Die-back of terminal sections of these branches was pronounced.

In his evaluation of the wasp at the first two release sites in the Cape Province, Dennill (1985) showed that within two generations the wasps had reduced seed production on galled branches by 99% and on heavily infested trees by 95% at the two sites, and that seed production was reduced by an average of 89% when 50% or more of the branches on plants of different sizes had galls. He further clearly showed that galls caused abscission of phyllodes (an actual decrease in the number over the season, rather than a net increase) and a 66% reduction in the number of new lateral branches/galled branch, and eventually a much higher (100%) growth tip mortality than on ungalled branches. On heavily infested trees, the same suppressing effect on growth tips and seed production was observed, whether there was only one or up to 72 galls/branch.

Figs. 1–6. *Acacia longifolia* (Andr.) Willd. and the gall-forming wasp, *Trichilogaster acaciaelongifoliae* (Froggatt). *1.* Dense regeneration of *A. longifolia* after a fire on the lower slopes of the Banhoek Mountains near Stellenbosch in the southwestern Cape. *2.* Female of *T. acaciaelongifoliae* ovipositing in a bud destined to develop into inflorescences 8–10 months later. *3.* Single and composite galls formed in axils where flower spikes would have developed. Fruiting on galled branches is usually entirely prevented. *4.* Section through a compound gall showing larvae and a pupa of *T. acaciaelongifoliae*. Up to 19 adults have been reared from a single, large, compound gall. *5. A. longifolia* heavily galled by *T. acaciaelongifoliae* at Geelong, Victoria (November 1982). Drought stress enhanced defoliation. *6.* Retarded galls on a heavily galled, largely defoliated plant (Geelong, November 1982). Similar levels of galling have been observed on odd branches at one release site at Stellenbosch (January 1984).

Observations on the very local and patchy distribution of the wasp in Australia may suggest that the species may be limited as an effective biological control agent by its supposed poor powers of dispersal. Noble (1940: 22) said: '... the adults are rather sluggish and degenerate in appearance. They crawl rather than fly and not uncommonly fall over and find difficulty in regaining their normal upright position.' Observations of newly emerged females on plants in the laboratory and in a glasshouse in 1981 and 1982 indicated that they are likely to disperse quite well, and may be capable of strong, and even directed flight in search of hosts. Newly emerged females, very distended with eggs, did not fly successfully, but after a few hours of egg-laying, and especially in the warmer part of the day, they readily took off on characteristic spiralling flights of many metres high, often returning to the *A. longifolia* plants in the vicinity. It is therefore quite likely that older females may fly, or be carried far during windy days and that with the high population densities anticipated, dispersal may be very effective.

In the population of *T. acaciaelongifoliae* from *A. longifolia* in Sydney studied by Noble (1940) males were rare, and absent in samples of galls from some plants. Flanders (1945), considering that the incidence of males was about 50% when apparently the same species from the same population developed in the vegetative and inflorescence buds on *A. floribunda*, suspected some form of 'environmental' control on the sex ratios.

During the present work, males were also found to be abundant in galls on *A. floribunda* collected in Victoria and Tasmania (in both instances the *A. floribunda* was planted together with, also galled, *A. longifolia*). However, the galls from *A. longifolia* from Launceston yielded unexpectedly large numbers of males. Another, larger sample (5 kg of galls) collected there in January 1984 yielded 887 females and 865 males. A colony established on *A. longifolia* on the slope of Stellenbosch Mountain from Launceston material collected January 1982, seems to perpetuate the phenomenon, as a sample of second generation galls collected there in December 1983 yielded 116 males and 64 females (but this last sample was taken when most wasps had emerged, and there is a possibility that males may tend to emerge later).

The males show interest in, and were seen to perform a relatively simple dance towards females, attempting copulation, and some observed attempts may have been successful. Noble (1940) showed that female offspring were produced by virgin females, but the effect of fertilization on the sex ratios in offspring has apparently not been studied.

Conclusions

On theoretical grounds, an insect developing in flower buds of a woody, long-lived legume growing at moist sites without much competition, and producing a staggering superabundance of inflorescences (usually two or more in nearly each phyllode axil on 1-yr-old branches on vigorously shooting plants) may not be readily seen as a very significant potential biological control agent, unless if used as a part of a complex complementing each other. Its potential value may even look less significant in the light of the longevity and the known formidable seed store in the soil in the infested areas (P.J. Pieterse, P.P.R.I. Stellenbosch, pers. comm.). However, the dramatic effect that this insect has been observed to have at such an early stage after release on seed production and vegetative growth (which would be expected to be enhanced by other adverse factors such as drought stress, as observed on the plants at Geelong in November 1982), and the fact that it may attack and multiply on young plants as soon as they start producing flower buds, indicate that this species by itself may in time be sufficient to cause a reduction in the density of infestations of the weed. The gradual expected suppression of the vigour of the plants and the accompanying thinning out of the otherwise dense canopies, may give other species a chance of establishing, and growing amongst the affected plants, and even to compete more successfully with them, thus adding another stress factor which may help to tip the balance in favour of the original vegetation in invaded areas.

The anticipated (and already observed) very heavy galling of plants in South Africa in the rather abnormal situation in the absence of its usual Australian parasitoids and competing species, may from time to time cause dramatic 'crashes' in the population of the wasp especially when the stressed host plant will not have sufficient resilience and reserves to allow full development of the galls and maturation of the larvae. The dynamics of the wasp populations and their effects on the plants and their populations in the next few years are likely to be most interesting, as will be comparisons of colonies in which the incidence of males differs.

Acknowledgments

The late S.E. Flanders, indirectly, through a publication on unisexual reproduction (Flanders 1945) drew my attention to the wasp of *A. longifolia* and gave the impetus to its further study. I should like to thank Dr. D.F. Waterhouse and Dr. Max Whitten of the CSIRO Division of Entomology, Canberra, for facilities offered to allow studies and collecting of the insect in Australia, and Ottilie Neser for valuable assistance. I am indebted to my colleague George Dennill for reading a draft of the manuscript.

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A Seed-feeding Insect Showing Promise in the Control of a Woody, Invasive Plant: the Weevil *Erytenna consputa* on *Hakea sericea* (Proteaceae) in South Africa

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Abstract

Hakea sericea, a fire-adapted woody plant from Australia, is an important weed in the species-rich vegetation of the Cape mountains. Prolific seeding may be regarded as the main reason for its success as an invasive plant. Larvae of *Erytenna consputa* destroy immature hakea fruits. The insect is strikingly adapted to its host and to surviving fires. The weevil was established in South Africa after the release of small numbers of field-collected, young adults from different climatic regions in Australia. Climatic matching was, however, not as important as host strain matching in the establishment of the weevil. Following establishment, *E. consputa* is greatly reducing seed accumulation by *H. sericea*, and starting to suppress the dense regeneration of the weed. Additional agents will probably not be required in the integrated control programme against this weed.

Les Insectes Granivores, Agents Efficaces de Lutte Biologique Contre les Plantes Ligneuses Envahissantes: Introduction du Charançon *Erytenna consputa* sur *Hakea sericea* (Proteaceae) en Afrique du Sud

Hakea sericea, une espèce australienne qui résiste aux incendies, est une important plante nuisible de la végétation très variée des montagnes Cape. La prolificité de ses graines est la principale cause de l'envahissement par cette plante. Les larves de *Erytenna consputa* détruisent ses fruits immatures, et l'insecte a une capacité exceptionnelle d'adaptation à son hôte et de résistance aux incendies. De petits nombres de jeunes adultes ont été recueillis dans diverses régions d'Australie pour être libérés en Afrique du Sud où ils se sont établis. Le climat n'a pas constitué un facteur déterminant dans l'établissement ou l'efficacité du charançon. L'élément le plus crucial était la lignée de plantes-hôtes sur lesquelles les insectes avaient été recueillis. Après son établissement, *E. consputa* s'est bien dispersée et a permis de réduire considérablement le nombre de graines de *H. sericea* et, par conséquent, la régénération des populations de plantes nuisibles incendiées. Il ne sera sans doute pas nécessaire de recourir a des agents supplémentaires pour assurer la lutte intégrée contre cette plantes nuisibles.

Introduction

Hakea sericea Schrader (Proteaceae) is a woody, perennial shrub from southeastern Australia. It was deliberately introduced into South Africa some 150 yrs ago and was initially widely planted in the southwestern to eastern Cape Province (Neser and Fugler 1978). It has since become naturalized, mainly in mountainous areas, over nearly half a million ha (Kluge 1983), often occurring in dense, impenetrable thickets. The seeds remain viable in woody follicles which accumulate over the years on the plant. It has been estimated that 75 million seeds/ha may be accumulated on 15-year-old stands of *H. sericea* (Kluge 1984). Following the death of the plant, usually after fire, all the seeds are released simultaneously. Neser (1968) regarded the prolific seed production of *H. sericea* in South Africa, in the absence of natural enemies, as the main reason for its invasiveness. This gives *H. sericea* a competitive advantage over the usually sparsely seeding native plants, and leads to more successful dispersal of the weed and to the establishment of its seedlings in niches that may have been occupied by the indigenous vegetation, or that may have remained vacant. Because of the adaptation of *H. sericea* to wind dispersal and to fires (accumulation of non-dormant, winged seeds that are released *en masse* after fires to germinate in the ash bed as soon as sufficient moisture is present), frequent fires favour *H. sericea* and lead to the rapid increase in density of the weed, to the point where the original vegetation is largely replaced and/or overshadowed.

From surveys of natural enemies in Australia (Neser 1968, 1984), two complementary seed-attacking species were selected and tested for release in South Africa. These are the weevil *Erytenna consputa* Pascoe (Coleoptera: Curculionidae) whose larvae develop in, and cause the death of, young fruits, and the moth *Carposina autologa* Meyrick (Lepidoptera: Carposinidae) that develops on seeds inside mature follicles accumulated on living plants (Neser and Annecke 1973; Neser and Kluge 1984). The aim of using seed-attackers was to reduce the numbers of seeds released after fires. This would allow the original vegetation to compete more successfully with regenerating *H. sericea* seedlings, and would help to prevent the occurrence of vacant niches where other invasive plants might get established if the hakea plants were removed too rapidly.

In this paper the establishment and effect of the first natural enemy to be successfully established, namely *E. consputa*, is considered, as are the attributes of the insect that contributed to its success, and to the important part it plays in the control of *H. sericea*.

Biology of *E. consputa*

The biology, phenology and host-specificity of *E. consputa* have been described by Neser (1968) and Kluge (1983). Adult weevils may live for two or three years, and are present on their host plant throughout the year, sheltering mostly in the dry husks of fruits attacked by larvae in previous seasons. They feed on buds and young growth, and on flowers and young fruits when these are available. Eggs are laid in or near young, developing fruits in spring and early summer. Larvae develop singly in, and destroy, one or more young fruits. A new generation of adults appears within three months, but eggs are only laid during the following fruiting season. Maturation of eggs in ovarioles is closely linked to the phenology of the host plant. Eggs are produced during the period when flowering and/or young fruits are present (Neser 1968). This effectively synchronizes hatching with the presence of immature fruits suitable to young larvae. Fecundated females are capable of producing fertile eggs in subsequent years without having to mate again, and may lay over 100 eggs/year (Kluge 1983). Adults are capable of strong flight, and may escape fires by flying off and locating surviving host plants from which they may colonize the next generation of seedlings. Even in the absence of live host plants, adults with a well developed fat body may survive for several weeks without food (Neser 1968).

Release and Establishment

Between 1971–81 about 8000 adult weevils were collected in Australia and released directly in small groups of 50–100 individuals/release at 126 sites throughout the *H. sericea*-infested area. The hakea infestations occur in areas with a Mediterranean-type climate (i.e. with dry summers) and extend into more temperate regions further east where the rainfall is more evenly distributed throughout the year. In an attempt to enhance the performance of weevils in different climatic regions in South Africa, releases were made with material from climatically similar areas in Australia.

E. consputa established successfully (i.e. colonies showed a consistent increase over at least four generations) at 80 of the sites, and at a monitored release site occurred over an area of about 9 ha after four generations (Kluge, unpubl. data). Extraneous factors such as accidental fires and clearing prevented establishment at 36 sites. *E. consputa* from the temperate Nerriga area in southeastern New South Wales established successfully at sites experiencing both temperate and Mediterranean-type climatic conditions. By contrast, the material from Wilson's Promontory in southern Victoria, where it rains predominantly in winter, established poorly. Eight of the ten releases where *E. consputa* failed to establish, for no apparent reason, were made with material from Wilson's Promontory.

In a 50 × 50 m study plot on a hakea-infested mountain slope at Goudini in the southwestern Cape, where a single release of only 20 *E. consputa* adults had been made in 1975, the annual fruit loss increased from 39% in 1979 to 81% in 1981. Concurrent studies on marked branches showed that the weevil was responsible for up to 86% of the total fruit mortality. A fire swept through this site in 1982 and 2 yrs later only 46 seedlings were counted in eight 0.5 × 50 m transects in which 459 plants had occurred before the fire (Kluge, unpubl. data).

Discussion

Somewhat surprisingly, insects from the temperate Nerriga area established readily in South Africa even in areas with arid summers. Since distinct strains of both *H. sericea* and *E. consputa* from different geographic areas in Australia have been recognized (Kluge 1983) it would seem that incompatibility of some strains with the form of *H. sericea* prevalent in South Africa, and not climatic matching, has been important in the establishment of *E. consputa* (Kluge, unpubl. data).

Reducing the seed crop reduces the number of seeds reaching any point in the distribution range of a plant (Harper 1977). From the widespread establishment of *E. consputa*, and the substantial seed loss reported here it can be concluded that the weevil is limiting the rate of spread of *H. sericea*. The reduction in plant density at the Goudini study site suggests furthermore that the level of seed predation being achieved by *E. consputa*, in combination with the high post-dispersal seed mortality as recorded by Richardson and van Wilgen (1984), is sufficient to reduce the density of subsequent *H. sericea* generations. This was the first demonstration of reduction in density of *H. sericea* after fire. In the past, before the introduction of *E. consputa*, weed density typically increased after fires.

The following attributes of *E. consputa* are considered to be important factors in its success as a biocontrol agent:

(a) Longevity and adaptation to survive fires. The regions in southeastern Australia where the insect originated and those in South Africa where its host plant became a serious weed problem are subjected to frequent fires. However, adult weevils are present on the plants throughout the year and have the ability to fly strongly, to find, and to survive on host plants that may escape the fires. They may also feed on non-fruiting seedlings until the latter reach the fruiting stage. This allows early colonization of young hakea infestations that develop after fires. Early colonization of young plants effectively reduces the accumulation of seeds on these plants, and eventually the density of regeneration of the weed after fire.

(b) The synchronization of egg-laying by females with the presence of fruits suitable for larval development maximizes damage to the fruit crop of the weed, even if the onset and duration of flowering varies from year to year and from place to place.

(c) The fact that females, after mating only once, are capable of producing normal complements of viable eggs for one or more years allows establishment of colonies even if females disperse widely. This may be an important contributing factor in the observed successes in establishing colonies of the insect with single releases of 20–50 adults.

(d) Once well established, population levels of the insect are related to, and eventually probably limited by, the number of fruits produced on the host plant. Superoviposition, for example, is not likely to result in a decrease of the number of individuals maturing on a given plant, as the larvae are cannibalistic. Populations of the weevil will be governed largely by fruit production of the weed, at a level where the attack of fruits may be maintained at 80% or higher judging by results from the study site. At this site the weevil population increased with the fruiting capacity of young plants (Kluge, unpubl. data).

Because of the large reduction in accumulated seeds brought about by the establishment of *E. consputa*, it is likely that the density of regenerating plants after fires, and thus of infestations, will gradually decrease, as demonstrated at the Goudini study site. Furthermore, if dense infestations are left as long as possible, many plants will die as a result of attack by the fungus *Colletotrichum gloeosporioides* (Penz.) Sacc. (Melanconiales) which is now known to cause severe mortality amongst *H. sericea* plants (Morris 1982, 1983). Where dense infestations are burnt or cleared manually after *E. consputa* has multiplied on them, and especially if refuges for the weevils in the form of surviving or deliberately protected plants are left, any regenerating seedlings will be subjected to early weevil attack.

Although the seed-attacking insects by themselves may not provide a quick solution to the hakea problem in South Africa, it is evident that they are already contributing to hakea control by suppressing further spread and by reducing the density of infestations around release sites. Their effect on seed production will also help prevent the recurrence of dense stands, thus obviating expensive follow-up work in areas that have been cleared mechanically. Furthermore the weevil is compatible with both the fungus *C. gloeosporioides* and mechanical clearing, and will become increasingly important in the three-pronged control programme against *H. sericea* (Kluge and Richardson 1983). Present indications are that additional natural enemies as suggested by Annecke and Neser (1977) will not be required.

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A New Era of Biological Weed Control in the Western United States

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Abstract

In recent years there has been a dramatic increase in interest, public support, and research activity in biological weed control in the Western Region of the United States. The marginal economic aspects associated with much of our rangeland, the limited effectiveness, increasingly high cost, concern for environmental impact, and the physical and legal limitation on the use of herbicides have fostered support for, and encouraged the development of, biological weed control programs within the between States. With the increase in cooperation between States, Federal biological control laboratories/agencies, and international biological weed control organizations and with the addition of a new insect quarantine facility at Montana State University in Bozeman, Montana, scheduled for completion in 1987, activities in biological weed control will reach greater heights than previously possible.

Ère Nouvelle dans la Lutte Biologique Contre les Plantes Nuisibles dans l'Ouest des États-Unis

Depuis quelques années l'ouest des États-Unis manifeste un intérêt de plus en plus marqué pour la lutte biologique contre les plantes nuisibles et intensifie les recherches dans ce domaine. Les aspects économiques marginaux de l'exploitation des pâturages, l'inefficacité, les restrictions d'utilisation, les coûts élevés et les préoccupations concernant les effets des herbicides sur l'environment sont autant de facteurs qui nous ont portés à appuyer et à encourager les programmes de lutte biologique contre les plantes nuisibles mis en oeuvre dans les états soit séparément soit en collaboration les uns avec les autres. Pour la première fois, divers états subventionnent le rassemblement à l'étranger d'ennemis naturels des plantes nuisibles et les essais de sélection. Grâce à la construction d'une nouvelle installation de quarantine des insectes à l'université du Montana à Bozeman, Montana, qui devrait être terminée en 1987, et à l'aide de APHIS/PPQ, un organisme de l'USDA qui se chargera de la redistribution des ressources dans l'ouest des États-Unis, la lutte biologique contre les plantes nuisibles réalisera des progrès sans précédent.

Introduction

In recent years there has been a dramatic increase in interest, public support, and research activity in biological weed control in the Western Region (Washington, Oregon, California, Idaho, Utah, Montana, Wyoming) of the United States. A number of factors have contributed to this change. The invasion and infestation of much of our rangeland by leafy spurge, *Euphorbia pseudovirgata* (*sensu* Ebke & McCarty) (Euphorbiaceae) (= former *E. esula* L.), and spotted and diffuse knapweed, *Centaurea maculosa* Lam. and *C. diffusa* Lam. (Compositae), respectively, have resulted in the reduction of favorable forage species and contributed to substantial losses in range productivity (Harris and Cranston 1979; Maddox 1979; Messersmith and Lym 1983). The consequences of reduced range productivity, the low market price for range livestock, and the slim profit margin realized per acre by the ranchers have put a premium on more economically feasible weed management strategies such as biological control (Maddox 1979; D. Woolworth, pers. comm., 1984). Furthermore, conventional weed control strategies such as chemical and cultural control, when applied in an economically feasible fashion, have proven ineffective in controlling some of our more noxious weeds of rangeland such as leafy spurge. As an example, conventional control efforts directed against well-established infestations of leafy spurge generally have resulted in only containment at best (B. Maxwell, pers. comm., 1984). The limited effectiveness (Lym and Messersmith 1983), increasingly high cost (Harris 1971; Maddox 1979; Schroeder 1983), concern for potential environmental consequences (Reichelderfer 1981; Andres and Clement 1984), and the physical and legal limitations on the use of herbicides have fostered support for, and encouraged the development of, biological weed control programs and/or projects within and between states. In recent years, faculty positions with responsibilities in biological weed control have been added to universities in Washington, Oregon, Idaho and Montana, with the associated development of respective biological weed control programs. In addition, the active participation by State Departments of Agriculture and the monetary support from the Forest Service have further signaled increased activity in biological weed control in the Western Region.

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Historical Development of Biological Weed Control in the Western Region

In tracing the historical development of biological weed control in the Western Region of the United States, one can cite the USDA and the University of California as being principally responsible for the initiation of biological control efforts against Klamath weed, *Hypericum perforatum* L. (Clusiaceae), during the mid-1900s and tansy ragwort, *Senecio jacobaea* L. (Compositae), during the 1960s. Initial responsibilities included collection, screening (host range and specificity tests), propagation, introduction and distribution of weed natural enemies. In addition, the USDA initiated numerous other projects on scotch broom, *Cytisus scoparius* (L.) Link. (Leguminosae), gorse, *Ulex europaeus* L. (Leguminosae), Italian thistle, *Carduus pycnocephalus* L. (Compositae), yellow starthistle, *Centaurea solstitialis* L. (Compositae), Mediterranean sage, *Salvia aethiopis* L. (Labiatae), dalmation toadflax, *Linaria dalmatica* (L.) Mill. (Scrophulariaceae), and other weeds during the late 1950s and early 1960s. With the early success realized in the biological control of prickly pear cactus, *Opuntia* spp. (Cactaceae), in Australia and Klamath weed in California, biological weed control became more and more respected as a viable weed management practice in rangeland. As new biological control projects were launched against leafy spurge, musk thistle, and spotted knapweed during the late 1960s and early 1970s the USDA's efforts were augmented by State cooperators who began to play an active role in the release and redistribution of natural enemies. As interest and activities in biological weed control grew, State cooperators began to meet annually with USDA personnel as participants of the Regional Research Project on Biological Control (W84), for purposes of coordinating research activities for biological control of insects and weeds.

Another important recent development has been the allocation of regional Cooperative State Research Service (CSRS) monies to the USDA Western Region, designated for purposes of developing and coordinating biological control activities for weeds of rangeland. In 1982, a Regional Biological Control of Weeds Committee was formed and consisted of USDA and State scientists from the western U.S., including Hawaii. Since that time, biological control personnel and weed scientists from the Western Region have had annual meetings to develop optimal plans for the utilization of these CSRS resources and the coordination of biological weed control activities. Some of the biological control projects funded to date by CSRS include: (1) rearing and redistribution efforts for insects attacking leafy spurge, spotted and diffuse knapweed, musk thistle, *Carduus nutans* L., Canada thistle, *Cirsium arvense* (L.) Scop., and dalmation toadflax; (2) collection and screening of insects and/or pathogens of leafy spurge and spotted knapweed; (3) a four-State (Washington, Oregon, Idhao, Montana) regional distribution and impact study of the seed-head flies, *Urophora affinis* Frld. and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on spotted knapweed seed production, plant biomass and plant density; and (4) a regional leafy spurge taxonomic effort utilizing the latest cytogenetic, chemical, and morphological taxonomic techniques and plant material from all western States with infestations of leafy spurge. In addition, the USDA Agricultural Research Service (ARS) has provided funding through cooperative agreement grants, for the collection and screening of insects and/or pathogens of leafy spurge, musk thistle, and yellow starthistle and for taxonomic studies of the European 'spurge' complex.

Another development that has helped increase the number of agents collected and screened for release against rangeland weeds has been the monetary contribution from States to the USDA and Commonwealth Institute of Biological Control (CIBC) foreign collection programs. To date, monetary contributions from Oregon, California, Idaho, Montana, Wyoming, and South Dakota have helped expedite the collection and testing of weed natural enemies and have helped insure that there are adequate numbers of natural enemies for release.

State support for biological weed control has taken other forms as well. The Montana Legislature in the last biennial session awarded $5.3 million to Montana State University at Bozeman to build a new Plant Growth Center and Insect Quarantine Facility, scheduled for completion in 1987. The new Plant Growth Center will give us year-round capabilities for growing plant material to sustain and propagate weed natural enemies and minimize the reliance on artificial diets. The Insect Quarantine Facility will complement the ongoing biological weed control activities at the USDA Biological Control of Weeds Laboratory in Albany, California. We will be able to aid them in freeing natural enemies of parasites and diseases and help in natural enemy host range and specificity tests on native plants from the region in which they will be released. We also will be able to rear actively weed control agents right out our back door under the environmental conditions and using plant material on which they will ultimately have to survive. The general intent of the Insect Quarantine Facility is to enhance biological control efforts in Montana and provide a regional natural enemy rearing service to States in the Western Region that share similar weed problems.

Another exciting development has been the desire expressed by APHIS/PPQ to actively participate in future rearing and redistribution of natural enemies of weeds in rangeland. This agency has already undertaken a project to locate spotted knapweed infestations using remote sensing techniques to target populations of the weed for later seed-head fly redistribution. The agency has also expressed an interest in possibly locating some of their personnel at Bozeman, Montana, to concentrate on rearing and redistribution of natural enemies on weeds in the Western Region.

And lastly, the increase in cooperation between States, Federal USDA laboratories/agencies and international biological control organizations has enhanced our abilities to: (1) receive and handle weed natural enemies; (2) document natural enemy impact and coordinate redistribution efforts on a regional basis; (3) better understand the type of weed problems we are faced with (through taxonomic and biological studies); (4) improve our chances of finding promising new natural enemies of weeds — both insects and plant pathogens; and (5) expedite host range and specificity testing of potential control agents on economically important plants and other desirable flora.

The USDA Biological Control of Weeds Laboratory in Albany, California, has played a vital role in screening, rearing, and distributing insect natural enemies of weeds to States in the Western Region. The development of improved communications between the States and this facility has helped us better plan for the receipt of new natural enemies and has allowed us to better synchronize the control agents with the appropriate stages of the weed. Through USDA/ARS Cooperative Agreement Projects with the Albany Laboratory and the USDA Plant Disease Research Laboratory, in Frederick, Maryland, States in the Western Region played an early role in the direction of biological control activities for the survey, collection, and screening of arthropod natural enemies of rush skeleton weed (*Chondrilla juncea* L.; Compositae) (Albany facility) and more recently for plant pathogens (Frederick facility) and insect natural enemies of yellow starthistle and leafy spurge.

International biological control agencies have also been helpful in the biological control of weeds effort. Agriculture Canada, primarily through the efforts centered at Regina, Saskatchewan, and the Albany Biological Control of Weeds Laboratory routinely apportion the various natural enemies destined for host-range and host-specificity testing to minimize unnecessary duplication and maximize the number of agents screened. The biological control laboratory at Regina has also been helpful in sending agents approved for release to States in the Western Region of the United States. Analogous to the relationship that has developed between the Albany and Regina biological control of weeds laboratories, the USDA Biological Control of Weeds Laboratory in Rome, Italy, CIBC, located in Delemont, Switzerland and the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) at Montpellier, France, have similarly delineated and coordinated their biological control activities. All three international laboratories have contributed greatly to the biological weed control effort in the Western Region. CIBC is currently involved in a project with Montana, CSRS, and Agriculture Canada to collect and determine the host range and host-specificity of key insects that attack spotted and diffuse knapweed. The Rome laboratory, in addition to their usual responsibilities of surveying, collecting, and screening of natural enemies of weeds, also have been helpful in collecting European leafy spurge plants, as has CIBC, in a cooperative effort with Montana, Agriculture Canada, domestic USDA laboratories, and other cooperating scientists to clarify taxonomically the European 'spurge' complex. In addition, CSIRO at Montpellier, France, was instrumental in the collection and/or screening of arthropod and pathogen natural enemies released against rush skeleton weed in Washington, Oregon, and Idaho. And lastly, another international cooperator that has recently become involved in a cooperative agreement project with the USDA Plant Disease Research Laboratory and Montana State University is the Institute für Phytomedizin in Zurich, Switzerland. Plant pathology researchers at this Institute are currently involved in the active search for plant pathogens of leafy spurge. They are currently conducting host-range and host-specificity tests on a promising systemic rust, *Uromyces scutellatus* (Uredinales), that attacks both leafy and cyprus spurge, *E. cyparissias* L. This Institute as well will be cooperating in the collection of European 'spurges' for taxonomic purposes, with the idea being that once we understand the extent of hybridization of this complex of plants then we may be able to match the type of plants that the natural enemies are collected from with similar plants in North America and thus more appropriately match up the natural enemies.

With all the cooperation and increased research activity that has developed in recent years between State, Federal, and international organizations, the framework and stage has been set for new advances in biological weed control.

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Biological Control of Weeds in Washington: Status Report

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Abstract

A summarization of biological control of weeds activities conducted in Washington since 1948 is presented. To date, 26 natural enemies have been released against 14 exotic weeds in the State. Of the organisms introduced, 18 (69%) have successfully become established. The role of natural enemies in suppressing population development of St. Johnswort (*Hypericum perforatum*), rush skeletonweed (*Chondrilla juncea*), tansy ragwort (*Senecio jacobaea*), and the knapweeds (*Centaurea* spp.) is discussed.

Lutte Biologique Contre les Plantes Nuisibles dans l'État de Washington

L'auteur fait brièvement l'historique de la lutte biologique contre les plantes nuisibles, entreprise dans l'état de Washington depuis 1948. A ce jour, 26 ennemis naturels de 14 plantes nuisibles exotiques ont été libérés dans l'état. Sur ce total, 18 organismes (69%) se sont établis. Le rapport traite du rôle des ennemis naturels de l'herbe squelette (*Chondrilla juncea*), des millepertuis perforés (*Hypericum perforatum*) et des séneçons Jacobée (*Senecio jacobaea*) dans l'élimination de ces mauvaises herbes ainsi que des programmes futurs de lutte biologique.

Introduction

During the past decade there has been increased interest in the biological method of weed suppression in the State of Washington. This interest has been stimulated by: several recent successful projects; continual increases in herbicide, fossil fuel and labor costs; herbicide toxicity concerns; increased demand for higher agricultural productivity; and the need to utilize marginally productive areas.

Most of the land in Washington is non-cropland. Such areas include non-irrigated pasture and rangeland, forests, highway and railroad right-of-ways, and vacant commercial and residential properties. Non-croplands are colonized by a diverse mixture of exotic and native weeds. Poisonous and unpalatable plants restrict land use for grazing and livestock production. Other weeds tend to limit natural reforestation by retarding seedling development of various timber species. Weeds of non-croplands frequently serve as alternate hosts for pest arthropods and plant pathogens which often invade agronomic or horticultural crops grown in the vicinity of the non-cultivated areas. Non-cropland weeds also are reservoirs of seed which is frequently transported into nearby agricultural or urban areas by man, animals, wind or water.

Over 50% of the noxious weeds occurring in non-cropland areas of Washington are exotics. These plants have attained undesirable densities primarily because they lack host-specific predators and pathogens which act as population regulators in the weeds' native homelands. In an effort to slow down or halt the often explosive increase of an alien weed, natural enemies are sought out in the weed's area of indigenity for eventual introduction into the invaded areas. This 'classical biological control' approach has been the only form of biological control utilized to date in Washington.

In recent years, several papers have appeared in the literature which summarize the status of biological control of weeds activities in North America (Goeden *et al.* 1974; Andres and Kok 1981) and elsewhere in the world (Goeden 1978; Julien 1982). Unfortunately, such accounts are usually incomplete due to the inability of the compilers to access all natural enemy release, establishment, and distribution records. In Washington, no comprehensive accounts of the progress of introduced weed-damaging organisms have been published heretofore even though this weed suppression method has been utilized since 1948. During the 36 years which have elapsed, 26 natural enemies have been imported and liberated against 14 alien plant species. Of these introduced agents, 18 (69%) have successfully established and contributed substantially to the non-cropland weed management effort.

Biological Control of Weeds Projects

St. Johnswort, Hypericum perforatum *L. (Clusiaceae)*

St. Johnswort, a plant of Eurasian origin, is a particularly troublesome weed in some areas of Washington. The weed is very aggressive and readily establishes itself in abandoned cropland, along transportation right-of-ways, and in open range grazing areas, greatly depreciating their carrying capacities through the displacement of desirable forage plants. St. Johnswort also may adversely affect livestock which feed upon it.

This weed has been successfully controlled in many areas with natural enemies (Goeden 1978). Two species of European leaf-feeding beetles, *Chrysolina hyperici* (Forster) and *C. quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae), were first released in Washington in 1948 for the control of the weed (Johansen 1957). Defoliation by *Chrysolina* adults and larvae decreases photosynthesis, which induces a decline in stored food reserves in the root, ultimately leading to plant death. Partial defoliation results in reduced plant vigor and loss of competitive ability (Holloway and Huffaker 1951). The beetles, particularly *C. quadrigemina*, have spread throughout the State and have markedly reduced *Hypericum* infestations.

In some areas, where for various reasons the beetles do not occur or are occasionally inhibited from attaining damaging levels, stands of St. Johnswort still persist. In such instances it is necessary to re-establish the beetles to effect control. Since 1979, nearly 362,000 adult *C. hyperici* and *C. quadrigemina* have been collected for redistribution to 11 counties in eastern Washington.

In 1954 and 1955 an unspecified number of adult *Agrilus hyperici* (Creutzer) (Coleoptera: Buprestidae) were released in Whitman County in southeastern Washington (Johansen 1957). This root-borer established, but populations have never reached large densities in those areas where it is known to occur. The impact of the insect on *H. perforatum* and its distribution in the State have not been ascertained.

In an effort to reduce St. Johnswort populations in beetle-impoverished areas and enhance weed suppression at *Chrysolina* spp. infested sites, field releases of the leaf bud gall-forming midge *Zeuxidiplosis giardi* Kieffer (Diptera: Cecidomyiidae) were made in 1955 in Pierce County in western Washington and in 1981, 1982, and 1983 in Whitman County, with all release stock originating in California. Gall presence inhibits the development of upright flowering shoots which results in decreased seed production.

Heavily galled plants suffer a notable loss of vigor and exhibit reduced foliage and root development (Wilson 1943; Holloway and Huffaker 1953). The midge readily galled potted plants grown in the greenhouse but failed to successfully colonize in the field when released. Additional importation of *Z. giardi* does not seem warranted at this time.

Rush Skeletonweed, Chondrilla juncea *L. (Compositae)*

Rush skeletonweed, a perennial plant native to central Asia and Europe, was inadvertently introduced into Washington during the late 1930s. The weed has since spread to infest over 810,000 ha of rangeland, semi-arid pasture land, transportation right-of-ways, residential properties, and croplands in eight eastern counties. Heaviest infestations are confined to rangeland where the weed displaces livestock and wildlife forage plants but encroachment of *C. juncea* into dryland wheat production areas has increased considerably in recent years. The plant's extensive root system enables it to effectively compete with crops for moisture and nutrients. The wiry, latex-exuding stems of mature plants can obstruct harvest machinery, making harvesting costly and difficult, if not impossible. Presently, two biotypes, designated 'Washington early-flowering' and 'Washington late-flowering', have been identified with the latter form being predominant in most infested areas.

Natural enemy releases were begun in 1976 and have been continued annually since 1978 in an effort to rapidly saturate rush skeletonweed infested sites with the control agents. Organisms released thus far include a rust fungus, *Puccinia chondrillina* (Bubak & Sydow) (Uredinales), a gall-forming midge, *Cystiphora schmidti* Rübsaamen (Diptera: Cecidomyiidae), and a gall-forming mite, *Eriophyes* (= *Aceria*) *chondrillae* (G. Canestrini) (Acarina: Eriophyidae).

The rust fungus attacks the seedling and regenerative rosettes produced during the fall and spring. Leaf surfaces become covered with numerous spore-containing pustules. As the rosette leaves die from infection, the pathogen attacks the stems, buds, and flowers (Hasan and Wapshere 1973). Open lesions produced as a consequence of spore formation cause desiccation, reduce photosynthetic surface area, and increase plant susceptibility to arthropod attack or other injury (Wapshere 1970, 1973). *P. chondrillina* most successfully controls seedlings and young plants which possess inadequate root reserves to permit re-establishment after attack (Adams 1982). Growth rate, root regenerative capacity, stem and bud production, and seed viability are reduced in older plants. Since 1979, over 100 releases of the fungus have been made in seven counties. Establishment and subsequent spore dissemination has occurred at over 90 release sites.

C. schmidti was initially released in Spokane County in 1976. The midge females deposit eggs in leaves and stems and blister-like galls develop around the plant-tissue-feeding larvae. Infested plants produce up to 63% fewer buds than do unattacked plants of comparable size and age (Mendes 1981). Seeds which are produced on attacked plants exhibit decreased viability and weigh less than seeds from healthy plants. Midge galls physically reduce the photosynthetic surface area of the almost leafless stems. This effect, combined with desiccation resulting from epidermal damage caused by emerging midges, leads to stunting, stem yellowing, and shoot-tip withering. When seedlings are heavily galled plant mortality usually results. Over 50 releases of the insect have been made thus far in all counties infested by the weed. The midge could be much more damaging to *C. juncea* if it were not for the presence of the parasitoid *Mesopolobus* sp. (Hymenoptera: Pteromalidae) which often destroys up to 95% of the late season midge populations (Wehling 1984).

The gall mite infests the developing vegetative and flower buds of rush skeletonweed, transforming them into leafy hyperplasic galls (Caresche and Wapshere 1974). The buds are completely destroyed as a result of gall formation, thereby curtailing seed production and in some instances totally suppressing it. Heavily galled plants exhibit premature chlorosis, are stunted with epinastic stem growth, and are unable to compete effectively with other vegetation. In excess of 100 releases have been made in seven counties. The mites have successfully colonized each site with no exceptions. *E. chondrillae* appears to be a highly effective biological control organism in Washington.

All agents attack the late-flowering biotype prevalent in the State but only the midge and mite can develop on the early-flowering form of the weed. Suppression of rush skeletonweed has been excellent in many areas and is expected to improve in other locations in time as the natural enemy populations increase.

Diffuse and Spotted Knapweed, Centaurea diffusa *Lam.,* C. maculosa *Lam. (Compositae)*

Diffuse and spotted knapweed are short-lived perennials of European origin that have become the most important rangeland weeds in Washington. These weeds jointly infest an estimated 400,000 ha in at least 20 of the State's 39 counties. Both species are of economic importance because they reduce forage production (up to 90%), decrease range carrying capacity, have little nutritive value for stock and wildlife, and form solid stands as a consequence of their allelopathic effects on indigenous and/or introduced grasses and forbs. Additionally, dense infestations, especially of diffuse knapweed, diminish wildlife habitat quality and often preclude utilization of large tracts of land for recreational purposes.

Biological control efforts against the knapweeds were begun in 1974 in Washington when 2400 adult *Urophora affinis* Frauenfeld (Diptera: Tephritidae) were released in Chelan, Kittitas and Okanogan Counties. another release consisting of 3100 adults was made in Chelan County in 1975. In 1979 and 1980, a total of 1672 adults were liberated in Spokane and Whitman Counties. All releases resulted in fly establishment with both knapweed species being utilized as hosts. Females deposit eggs into developing flower heads and the larvae induce gall formation within the heads. The larvae feed on nutritive cells which line the gall interior. These cells increase the size of the metabolic sink in the seed head so that the plant supplies more nutrients to attacked heads. A reduction in the amount of nutrients available for plant growth and development results which is expressed as terminal or lateral bud abortion, reduced seed production, and decreased seed viability (Harris 1980). *U. affinis* presently occurs in 12 of the 20 knapweed-infested counties east of the Cascade Mountains.

U. quadrifasciata (Meigen), another seed-head gall fly, was first discovered in Spokane County in 1979. The insect invaded the State from British Columbia where Canadian weed control specialists had previously made releases and it now can be found in all counties east of the Cascades. Larvae attack the floral ovaries, transforming them into papery-thin galls. Damage to both knapweed species is similar to that produced by *U. affinis*. Since 1980, redistributions of this species have been made to south-central and eastern Washington counties where fly densities are still somewhat low.

According to Harris (1980), both *U. affinis* and *U. quadrifasciata* have reduced seed production by 95% in Canada since their release in that country 14 years ago. A study is presently being conducted in Washington to quantitatively assess the impact of the flies on populations of *C. diffusa* and *C. maculosa*.

Sphenoptera jugoslavica Obenberger (Coleoptera: Buprestidae), the larvae of which feed in the taproot of diffuse knapweed and cause galls to develop which structurally weaken the root and reduce plant vigor (Zwölfer 1976), has been introduced into the State. Twenty-seven adults were released in Spokane County in 1980, 47 adults in Okanogan County in 1983, and 48 adults in Whitman County in 1984. No establishment was recorded for the 1980 release and the remaining release areas have not been sampled to determine beetle presence or absence.

In 1981, 810 adult *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae) were released in Spokane and Whitman Counties on spotted knapweed. The moth larvae feed upon the developing florets and seeds in the flower heads, consuming most of the seeds in the head (Englert 1971). Establishment was confirmed at both sites in 1982 and redistribution of *Metzneria* to other areas began in 1984.

Russian Thistle, Salsola iberica *Sennen & Pau (Chenopodiaceae)*

Russian thistle or tumbleweed, indigenous to southeastern Russia and western Siberia, is a multibranched annual that occurs throughout much of eastern and central Washington. The plant's efficient root system, abundant seed production, reduced leaf surface, and photosynthesizing branches well adapt it to disturbed, semi-arid agricultural environments where it competes with more desirable plants for water and nutrients.

Natural enemy introductions were started in 1979. At a site in Whitman County, 353 *Coleophora klimeschiella* Toll (Lepidoptera: Coleophoridae), the larvae of which feed both internally and externally upon the leaves and cause damage especially during the weed's early developmental stages (Khan and Baloch 1976), were colonized. During 1980 and 1981, 46 and 1000 additional individuals, respectively, were released at the same site. Establishment has been achieved but moth populations remain low and no discernible reduction in weed density has been observed.

A second coleophorid species, *C. parthenica* Meyrick, whose larvae tunnel the stems and branches (Hawkes and Mayfield 1976) contributing to reduced seed production and viability, stunting, or even death, was released in 1979, 1980, and 1981 (133, 48, and 64 individuals, respectively). This insect did not establish in Washington and no further releases are contemplated.

Musk Thistle, Carduus thoermeri *Weinmann (Compositae)*

This European plant is a serious biennial or winter annual of overgrazed pastures and rangeland in several eastern Washington counties. Although effective chemical suppressants are available, they are costly and must be repeated to eliminate plants developing from seed in the soil.

The seed-head weevil, *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae), was first released in the State in 1982. Approximately 5000 adults were collected near Belgrade, Montana, and distributed to Okanogan and Walla Walla Counties for release on musk thistle. Establishment was confirmed in 1983. Adults released in isolated stands of *Cirsium arvense* (L.) Scop., *C. undulatum* (Nutt.) Spreng., and *Onopordum acanthium* L. (all Compositae), all previously reported hosts for *R. conicus* (Rees 1978), failed to colonize.

In 1983, 25,585 adults were again obtained from Montana and transported to Ferry, Okanogan, Stevens, and Walla Walla Counties to enhance existing weevil populations or to initiate new infestations, especially in Ferry and Stevens Counties. A check of the release sites in these areas revealed musk thistle was being utilized by *R. conicus*. At another site in Stevens County, 2000 adults were placed on plumeless thistle, *Carduus acanthoides* L. The status of this release has not yet been determined.

Canada Thistle, Cirsium arvense

Canada thistle, a weed of Eurasian origin, is the most widespread and important noxious weed infesting cropland and non-cropland areas in Washington. The obnoxious character of this plant is due primarily to the highly successful vegetative propagation carried on by the creeping horizontal roots which survive perennially and give rise to numerous aerial shoots.

The first insect introduced specifically for *C. arvense* control was *Altica carduorum* Guérin-Méneville (Coleoptera: Chrysomelidae). Two hundred individuals were released in Whitman County in 1966 followed by the release of 106 additional beetles in 1968. As no evaluation studies were ever conducted and no progeny ever collected, it may be assumed that the releases failed. No subsequent importations were made.

In 1974 the first release of *Ceutorhynchus litura* (F.) (Coleoptera: Curculionidae) was made in Benton County. The larvae of this weevil mine rosette leaves and young shoots of plants. The 200 adults released failed to establish at the site. In 1984 a decision was made to try to establish the beetle once again. A shipment of 100 adults was received from California and released in Whitman County.

Urophora cardui (L.) (Diptera: Tephritidae), whose larvae induce the formation of galls in primary or secondary stems, shows promise for the biological control of Canada thistle. Gall development prevents seed production and disrupts the vascular system, causing a reduction in plant biomass and vigor (Peschken and Harris 1975; Shorthouse and Watson 1976). The fly was first liberated in 1982 in Whitman (375 adults) and San Juan (181 adults) Counties. Establishment was confirmed for Whitman County only, the flies producing 1–3 galls/plant during the year of the release. A total of 422 galls were removed from the site in the spring of 1983 and held in the laboratory to yield 1174 adults. These flies were divided into variously sized allotments and released in eight counties across the State. The tephritid was able to colonize successfully five of the areas. Additional releases of 686 adults were made in three counties in 1984. No impact studies have been undertaken yet to assess the agent's damage potential under Washington conditions.

Bull Thistle, Cirsium vulgare *(Savi) Tenore (Compositae)*

This plant, an introduced European native, is a nuisance in grazed pastures, rangland, logged areas, wasteland, and along transportation right-of-ways. In 1983 the seed-head-damaging fly *Urophora stylata* L. (Diptera: Tephritidae) was obtained from Canada for release in eastern Washington. Females deposit eggs in unopened buds and the larvae destroy floral tissue and feed on developing seeds. Thick-walled galls surround the larvae in the receptacle. The presence of *U. stylata* may reduce seed production by 60% (Persson 1963; Schroeder 1980).

In 1983, 1300 adults were released at three sites in Whitman County and 600 adults at two sites in Klickitat County in south-central Washington. Establishment occurred at all release sites. In 1984, 172 flies were distributed amongst two sites in Whitman County and another 240 were set free at a site in Spokane County.

Puncturevine, Tribulus terrestris *L. (Zygophyllaceae)*

This annual plant, native to the Mediterranean area, is a pest of cultivated fields, waste areas and utility right-of-ways. The weed produces many seeds which are contained within spined fruits. These fruits interfere with hand-harvesting of crops, cause a downgrading of agricultural products, and may injure the mouths and digestive tracts of livestock upon ingestion (Johnson 1932).

The seed weevil, *Microlarinus lareynii* (Jacquelin du Val), and the stem weevil, *M. lypriformis* (Wollaston) (Coleoptera: Curculionidae), were introduced from Italy to control puncturevine. *M. lareynii* larvae feed upon the developing seeds while the larvae of *M. lypriformis* tunnel the stems (Kirkland and Goeden 1978*a*, *b*). High larval populations reduce plant size and the quantity of seeds produced. Both species are established in the United States and have reduced the abundance of the weed (Maddox 1976).

Releases of weevils field-collected in Italy were made in 1961 in Washington. In Benton County, 209 adult *M. lareynii* and 88 *M. lypriformis* were released. Another release of 100 *M. lareynii* adults was made in Frankilin County at the same time. Establishment was not achieved at the sites (Maddox 1976). In 1963, a total of 400 adult *M. lareynii* and *M. lypriformis* field-collected in California were distributed in Grant County. This release also failed. Apparently the curculionids were unable to survive the harsh eastern Washington winter weather.

In 1982, cold-tolerant biotypes of both species were obtained from Colorado and released in Whitman County. No plant injury was observed following the liberation of 189 individuals and no evidence of establishment was found in 1983. Further attempts will be made to establish *Microlarinus* spp. in Washington.

Dalmation Toadflax, Linaria dalmatica *(L.) Miller (Scrophulariaceae)*

Dalmation toadflax, a short-lived perennial herb native to the Mediterranean, has become a serious weed of disturbed soils and depleted rangelands. Livestock generally avoid eating the weed and several plants/m^2 reduce the yield of grasses and forbs by 50–60% (Polunin 1969).

Calophasia lunula (Hufnagel) (Lepidoptera: Noctuidae), utilized in Canada in the 1960s for control of butter-and-eggs, *Linaria vulgaris* Miller, and Dalmation toadflax, was initially obtained for release in Washington in 1968. Moth larvae consume the foliage, floral buds, and flowers. Feeding damage reduces seed production, halts photosynthesis and depletes carbohydrate reserves in the roots, thereby lessening the plant's competitive ability.

A release of 250 larvae was made in Spokane County at several sites during 1968 and another release of 200 larvae was made in the same County the following year. No establishment occurred at any site where the moths were liberated. In 1970, at an *L. dalmatica* infested site in Whitman County, 185 larvae were released. No insect activity was discernible at the site the following year.

Another attempt to establish *C. lunula* was made in 1982. A total of 450 larvae were released in Spokane County at three sites, 325 larvae in Klickitat County, 171 larvae in Ferry County, and 100 larvae in Yakima County. The natural enemy did not establish at any site even though feeding on Dalmation toadflax was observed in the field following the releases. In 1983 another 100 larvae were released in Spokane County but no progeny could be located in the vicinity of the release during 1984.

Gorse, Ulex europaeus *L. (Leguminosae)*

Gorse is a densely-branched, spiny shrub which grows primarily in coastal areas in western Washington. The plant spreads rapidly in burned-over timber or brush areas, preventing the return of native forage plants as well as conifers, thus greatly interfering with reforestation efforts.

In 1964, the gorse seed weevil, *Apion ulicis* Forster (Coleoptera: Culculoinidae), was introduced to decrease the rate of spread of the plant. Larvae of the insect inhabit the seed pods and eat the developing seeds. Seed crop reductions in excess of 95% have been realized at some sites. A release of 765 adults was made in San Juan County and dispersal of *A. ulicis* from the release area to other gorse infestations has transpired during the past two decades.

Russian Knapweed, Centaurea (Acroptilon) repens *(L.) DC. (Compositae)*

This plant, a native of Asia, forms dense infestations in Washington pastures, along transportation right-of-ways, along irrigation ditches and agricultural field borders, and sometimes invades cereal grain and alfalfa fields. The weed spreads primarily via its creeping horizontal root system but also by seed to some extent.

In the plant's native homeland, it is frequently damaged by the nematode *Paranguina picridis* Kirjanova & Ivanova (Nematoda: Tylenchidae). The first attempt to establish this organism in Washington was made in 1984 with material supplied from Canadian biological control cooperators. The nematode penetrates the emergent shoots of Russian knapweed in the spring and its presence leads to gall development on the root crown, stems, and leaves. Infected plants are severely distorted and stunted and reproduction by seed or vegetative means is reduced (Ivanova 1966).

Two releases of the organism were made in Okanogan County. Examination of the sites several months after the releases revealed the presence of *P. picridis* but only a small number of plants were infected at the sites. It is unknown whether the nematode will be able to successfully overwinter under Washington conditions.

Tansy Ragwort, Senecio jacobaea *L. (Compositae)*

Tansy ragwort, a European biennial or short-lived perennial, is a major noxious weed of poor quality pasture and range areas throughout most of the counties west of the Cascades in Washington. *S. jacobaea* displaces desirable forage plants and is also toxic to cattle and horses. Pyrrolizidine alkaloids in the plant, when consumed by livestock, produce progressive and irreversible liver damage.

The cinnabar moth, *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae), was first released in Washington in 1960. During the decade that followed, thousands of larvae were released amongst infestations of the weed. Larvae feed on leaves, buds, and flowers, frequently defoliating all plants in an area. The insect presently can be found in most tansy ragwort-infested sites in the State and annual redistributions are carried out by noxious weed control personnel.

A second organism was introduced for the control of this weed in 1968. The ragwort-seed-head fly, *Hylemya seneciella* Meade (Diptera: Muscidae), whose larvae feed within the floral buds consuming the developing seeds, was released in Clark County (3348 adults) (Frick 1969). Field recovery of individuals was made later the same year. A search of the release site and surrounding area during succeeding years failed to provide evidence for fly survival. During 1981, tansy ragwort damaged flower heads were brought in to county extension agents by several landowners in southwestern Washington. An examination of the areas where the plants had been found revealed that *H. seneciella* was well-established and was destroying *c.* 30% of the seed heads produced.

The last insect species to be imported into the State for tansy ragwort suppression was the ragwort flea beetle, *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae). Adults damage foliage in fall, and larvae feed in the root crown and rosette leaf petioles during fall and spring causing extensive damage. Releases of several thousand adults were made in various southwestern Washington counties during 1970, 1972, 1974, and 1975. *L. jacobaeae* is now well-established and has effectively reduced tansy ragwort population by itself or more frequently complements the damage inflicted by the cinnabar moth and/or ragwort seed fly.

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The Place of Biological Control of Field Bindweed in California's Coastal Vineyards*

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Abstract

Field bindweed, *Convolvulus arvensis*, is a dominant member of the weed community and the principal plant pest in California's coastal vineyards. Its biological control potential was studied in four of them. Defoliators cause considerable damage, but none appear suitable as biological control agents. Some arthropods, such as *Noctuelia floralis*, associated with field bindweed stems in Eurasia, could be useful in California vineyards. Others which feed on closely related native plants or sweet potatoes are unsuitable for California, but may be of value in parts of the world where no such conflicts of interest exist. Exotic leaf and bud galling Eriophyidae which are lacking on field bindweed in California would be particularly appropriate for importation to control the weed. As other Eriophyidae already occur on native North American morning glories yet have not transferred to field bindweed, exotic gall mites are not likely to switch hosts and damage the native flora. More research on pathogens for augmentative biological controls is needed. Use of biological control against field bindweed in pest management programs would be feasible for vineyards and, perhaps, orchards under present systems of cultivation. Greater acceptance of some weed growth and changes in existing pest controls, such as the substitution of other chemicals for sulphur, would enhance biological control effectiveness.

Possibilités de Lutte Biologique Contre le Liseron des Champs dans les Vignobles de la Côte de la Californie

Les possibilités de lutte biologique contre le liseron des champs, *Convolvulus arvensis*, ont été étudiées dans quatre vignobles situés le long de la côte californienne, où cette espèce est la principale plante nuisible et celle qui prédomine dans la communauté des plantes nuisibles. Les chenilles défoliatrices et les tétranyques endommagent considérablement cette plante nuisible, mais aucun de ces insectes ne semble efficace comme agent biologique. Toutefois, certains arthropodes comme *Noctuelia floralis*, associés au liseron des champs en Eurasie, pourraient être utiles dans les vignobles de Californie. D'autres arthropodes, qui ne peuvent être employés en Californie puisqu'ils se nourrissent de plantes indigènes étroitement apparentées ou de patates douces, pourraient sans doute servir dans d'autres parties du monde où ces conflits d'intérêts n'existent pas. Il serait possible d'avoir recours à des méthodes de lutte biologique contre le liseron des champs dans le cadre de programmes d'élimination des plantes nuisibles dans les vignobles et peut-être aussi dans les vergers, compte tenu des systèmes de culture actuels. La lutte biologique pourrait être plus efficace si la croissance d'un certain nombre de plantes nuisibles était mieux acceptée et si les techniques actuelles de lutte contre les ravageurs étaient modifiées.

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Candidate Insects for the Biological Control of *Rumex pulcher*

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Abstract

Rumex pulcher (Polygonaceae) is a major weed of pastures in Mediterranean-like climatic regions of southwestern Australia. The origin of the plant is probably the Mediterranean area and a search was made in the western part of this region for insects that attack the weed. Nine of the species found during this survey were selected for further study. Those judged most suitable for biological control purposes were the sesiid moths, *Bembecia chrysidiformis* and *Chamaesphecia doryliformis*. Larvae of these insects feed in the root, often causing death of the plant. The root-feeding weevil, *Lixomorphus ocularis*, and the stem-feeding weevils, *Apion (Perapion) violaceum*, *A.* (*Perapion*) *hydrolapathi*, *A.* (*Erythrapion*) *miniatum*, and *Lixus ferrugatus*, and the leaf-mining flies, *Pegomya bicolor* Wied. and *P. nigritarsis*, are also being studied but are considered to be of lesser importance or possibly unsuitable for biological control purposes depending on future work. Most of these insects feed widely on species of the subgenus *Rumex* and hence there is a possibility of Australian native *Rumex* of the same subgenus being attacked. This conflict of interest will need to be resolved before importations can be made.

Insectes Choisis pour la Lutte Biologique Contre *Rumex pulcher*

Rumex pulcher (Polygonacées) est une des principales plantes nuisibles des pâturages des régions à climat méditerranéen, du sud-ouest de l'Australie. La plante est sans doute originaire de la région méditerranéenne où on a effectué des fouilles pour trouver des insectes qui détruiraient cette plante nuisible. Parmi les espèces étudiées, on en a retenu huit en vue d'analyses supplémentaires. D'après les résultats, les sésies, *Bembecia chrysidiformis* et *Chamaesphecia doryliformis* constituent les agents biologiques les plus appropriés. Ces insectes, qui sont racidivores, entraînent souvent la mort des plantes. En outre, d'après la documentation et les essais de spécificité d'hôte, les sésies ne vivent que sur les plantes du sous-genre *Rumex*. Le charançon racidivore *Lixomorphus ocularis*, les charançons mangeurs de tiges *Apion* (*Perapion*) *violaceum*, *A.* (*Perapion*) *hydrolathium*, *A.* (*Erthrapion*) *miniatum*, et *Lixus ferrugatas*, et les mineuses des feuilles *Pegomya nigritarsis* et *P. bicolor* Wied. ont aussi été étudiées, mais sont moins efficaces ou ne se prêtent pas à la lutte biologique. Étant donné que la majorité de ces insectes ne choisissent que des plantes hôtes du sous-genre *Rumex*, les espèces indigènes du même sous-genre d'Australie risquent aussi d'être infestées. Ce conflit d'intérêts devra êtra réglé avant d'importer les insectes.

Introduction

Rumex pulcher L. (Polygonaceae) is a major weed in the Mediterranean-like climatic regions of southwestern Australia, which has proved difficult to control by chemical and cultural means (Allen 1974, 1975). Since *R. pulcher* is an introduced weed in Australia, it was decided by the Western Australia Department of Agriculture to investigate possibilities for biological control of this weed. The study started in late 1981 and concentrated on phytophagous insects in western Mediterranean countries. This region is the probable area of origin of the plant. This paper reviews the progress so far with this study.

Rumex species, but not *R. pulcher*, have been examined previously for biological control agents. A list of insects and pathogens, mainly from Italy, has been given for *R. crispus* L. with initial biological studies made of *Bembecia chrysidiformis* (Esper) (Lepidoptera: Sesiidae) and *Lixomorphus ocularis* F. (Coleoptera: Curculionidae) (Spencer 1981). An examination of the host plant specificity has also been made of the fungus *Uromyces rumicis* (Schum.) Wint. (Uredinales) on *R. crispus* (Frank 1973; Inman 1971). A list of possible biological control agents amongst fungi which attack the genus *Rumex* is given by Sedlar *et al.* (1983).

Two studies on biological weed control within the country of origin have been made on *R. obtusifolius* L. Garcia-Baudin and Santiago-Alvarez (1978) report on *Gastrophysa unicolor* Marsham (Coleoptera: Chrysomelidae) in Spain, and a list of insects (Miyazaki 1979) and a detailed study of *G. atrocyanea* Mots. (summarised in Miyazaki and Naito 1981) has been given for Japan.

Finally the Commonwealth Institute of Biological Control has examined a number of *Rumex* species in Pakistan in a search for biological control agents (CIBC, unpubl. repts.). None of the above studies have resulted in the release of insects or pathogens in countries where *Rumex* is a problem. The only releases of insects known to attack *Rumex* have been made for biological control of *Emex* spp. (Polygonaceae) (Julien 1981; Julien *et al.* 1984). However *Rumex* has not been reported to be attacked in the countries of release.

Preliminary Investigations

Taxonomy of the Weed

Rumex is a world-wide genus of about 160 species divided into four subgenera: *Acetosa*, *Acetosella*, *Platypodium* and *Rumex*, the latter including *R. pulcher* as well as the weeds *R. crispus* and *R. obtusifolius*. The Australian continent has representatives of all four subgenera amongst a total of 17 species. Eight species are native and all belong to the subgenus *Rumex* (Rechinger 1984). *R. pulcher* belongs to the section *Simplices*, subsection *Obtusifolii* and has five subspecies but only two, *R. pulcher pulcher* and *R. pulcher divaricatus* (L.) Murb. occur in Australia (Rechinger 1984). Both subspecies are weeds in southwestern Australia but *R. pulcher divaricatus* appears to be the most important. This subspecies is typical of the Mediterranean region and is now widespread in areas of similar climate throughout the world. *R. pulcher pulcher* has a similar distribution and Rechinger (1984) observes that in some cases there is not a clear distinction between the two subspecies.

Biology and Economic Importance

The biology of *R. pulcher* largely remains undescribed. There should however be a number of similarities with the well-known species *R. crispus* and *R. obtusifolius*, which are also taxonomically closely related to *R. pulcher*.

One of the few studies of *R. pulcher* has been by Allen (1974), who established that this weed was the dominant *Rumex* species in pastures of southwestern Australia, except in wetter areas, where *R. crispus* was found. *R. pulcher* over-summers as a root stock and underground stem which produces leaves in early autumn, remains as a rosette through winter, with inflorescences appearing in spring. Seedlings appear throughout the growing season. The plant is perennial but the longevity is unknown.

Allen (1974) suggests that cultivation, which exposes the root stock to desiccation, would kill the plant. However he notes that the plants will regrow from severed root stocks in autumn. Allen (1975) suggests the following control techniques: replacing cattle with sheep; establishing perennial grasses; and cropping, followed by a herbicide treatment. However these techniques are not practical in areas where cattle graze on annual legume-based pastures. Other alternatives were the use of low-dose herbicides followed by heavy grazing 1 wk later. However, herbicide treatment is usually detrimental to the legume which is the basis of the pasture. Overall, *Rumex* species were estimated to cost farmers $A400,000 p.a. in lost production (Allen 1975). Recently McGhie *et al.* (1983) suggested that *Rumex* species in pastures of southwestern Australia may be useful as feed for sheep early in the growing season and of doubtful usefulness late in the season and when mixed with hay.

Possible Biological Control Agents

Thirty-seven species of phytophagous insects were found feeding on *R. pulcher* during a search of the western Mediterranean region (southern France, including Corsica; Italy, including Sardinia and Sicily; Spain, Portugal, and Morocco) (Scott and Sagliocco, unpubl. data). Nine of these species were selected for further study after a consideration of pubished host plant records. Each of these species is considered below.

Apion (Perapion) hydrolapathi *Marsham (Coleoptera: Apionidae)*

Larvae of this weevil bore inside the stem and petioles; adults feed externally on leaves, petioles and stems of *Rumex* species. It is found throughout the littoral regions of Europe and the Mediterranean and has been recorded from *R. crispus*, *R. hydrolapathum* Hudson, *R. pulcher* (Hoffmann 1958) and *R. obtusifolius* (Radde 1974). This species is difficult to separate from *A.* (*Perapion*) *violaceum*, being morphologically and biologically similar. Work is needed to clearly differentiate these species before *A. hydrolapathi* can be considered for use in biological control.

Apion (Perapion) violaceum *Kirby (Coleoptera: Apionidae)*

As with the previous species, *A. violaceum* has larvae which bore inside the stem and petiole, and adults which feed externally on above-ground parts of many different *Rumex* species, chiefly of the subgenus *Rumex* (Hoffmann 1958). The insect is widely distributed in Europe and the circum Mediterranean region. The biology of the species in the Montpellier region of southern France has been examined (Scott, unpubl. data), and preliminary host-specificity tests have been made with a range of plants mainly from the Polygonaceae. Adults were found to feed on *Rumex* species, *Emex spinosa* (L.) Campd., *Rheum rhabarbarum* L. (Polygonaceae) and *Fagopyrum esculentum* Moench (Polygonaceae); eggs were laid on *Rumex* species, *E. spinosa* and *R. rhabarbarum*; and larvae developed on *Rumex* species and *E. spinosa*, but died in the first instar on *R. rhabarbarum*. An Australian native species, *R. dumosus* A. Cunn. ex Meisn., was amongst the most heavily attacked of the *Rumex* species. It remains to be seen if this insect can complete a whole generation on these plants, especially the Australian native *Rumex* species.

Apion (Erythrapion) miniatum *Germar (Coleoptera: Apionidae)*

This weevil has larvae which feed in the lower stems of *Rumex* species; adults feed on leaves. It is widely distributed in Europe and the Middle East (Hoffmann 1958). This insect is not abundant and hence little study has been made of its biology and host plant specificity.

Lixomorphus ocularis *(F.) (Coleoptera: Curculionidae)*

Presence of larvae of *L. ocularis* (F.) inside roots of *R. crispus* was discovered and its biology briefly described by Spencer (1981). Previously its biology was unknown (Hoffmann 1950). Following from Spencer's work, Cassobasso and Murano (pers. comm.) have made a detailed study of its biology. The weevil's distribution is Algeria, Spain, Italy and Corsica (Hoffmann 1950). Its only known host plants are *R. crispus* (Spencer 1981) and *R. pulcher* (Scott and Sagliocco, unpubl. data). Spencer (1981) found no feeding preference for adults caged on *F. esculentum*, *R. rhabarbarum*, *R. crispus*, *R. acetosa* L., *R. scutatus* L., and *R. conglomeratus* Murray. In no-choice tests carried out in Montpellier, adults from Corsica fed readily on leaves of *R. pulcher*, *R. conglomeratus* and *R. acetosa*, and light feeding occurred on *R. rhabarbarum*; test bites were found on *R. obtusifolius*, *Daucus carota* L. (Umbelliferae) and *Beta vulgaris* L. (Chenopodiaceae). Both the above sets of tests were of a preliminary nature and consequently it is not possible to state the host-plant range of this insect.

Spencer (1981) considered that this species would not be a suitable biological control agent based on its biology and host-specificity tests. However more detailed work, especially on the feeding preference of larvae is needed.

Lixus ferrugatus *Olivier (Coleoptera: Curculionidae)*

Both the above name and *L. cribricollis* Boheman have been used for this weevil which has been introduced into Australia for the biological control of *Emex* species. In host plant specificity tests, *R. crispus* was found to be attacked by populations of the weevil from Morocco (Julien *et al.* 1984). Hence it is not surprising to find that it feeds on *Rumex* species in the northern part of this insect's range, where *Emex* does not occur.

Insects of this species which attack *Rumex* could be considered for introduction into Australia after assessing the success of the insects from Morocco. This large weevil (up to 14 mm long) is found throughout central and southern Europe, Algeria, Morocco and the Middle East (Hoffmann 1954). Its biology is described by Julien *et al.* (1984). Larvae make tunnels in flowering stems of *Emex* and *Rumex* species during May to July. The weevil is rare in the Montpellier region, but attacks mainly *R. pulcher*. However, the amount of damage inflicted seemed slight, as the insect lays eggs only when the flowering stem is well-developed (Scott, unpubl. data). This behaviour exists presumably so that the larvae will have sufficient material to complete development. Hence, it is doubtful, given this attack phenology, that this insect could reduce the plant population, given the densities of insects observed around Montpellier. However, once released in Australia the population density may well be different, and damage to plants may reduce seed production. Hence this insect should be re-examined to determine: (1) the extent of establishment in Australia, especially on *Rumex*; (2) the amount of damage caused to *Rumex* plants in nature and caged environments; and (3) if the host plant specificity of this insect on *Rumex* species and other Polygonaceae is the same as the population from *Emex* described in Julien *et al.* (1984).

Bembecia chrysidiformis *(Esper) (Lepidoptera: Sesiidae)*

This clearwing moth was initially considered for the biological control of *R. crispus* (Spencer 1981). The larvae feed inside the root and underground stem of the plant. In addition to *R. crispus*, this insect is known to attack *R. acetosa* (Popescu-Gorj *et al.* 1958) and was found in this survey in *R. pulcher*, *R. obtusifolius* and *R. conglomeratus*.

Host plant records of *Artemisia campestris* L. (Compositae) and *Helichrysum* sp. (Compositae) (Popescu-Gorj *et al.* 1958) are most probably erroneous. Adults may feed on nectar in flowers of these plants, which may have lead to the assumption that the plant was also the larval food plant. *A. campestris* has also not been attacked in host-specificity tests with larvae from France and Portugal (Scott and Sagliocco, unpubl. data).

Adults emerge from pupae at the start of summer, mate, and lay eggs onto stems of *Rumex* plants that have flowered that year. After 6–12 days, depending on temperature, larvae eclose and climb down the stem to enter the plant about 1 cm below the soil. All subsequent development takes place within the root or the underground stem. By 2 wks larvae are in the third instar, and larval development is probably finished by the end of summer. By this time the root has been largely destroyed. Larvae pass winter in a silk-lined sack and pupate in mid- to late-spring. Adults feed on nectar of flowers.

Usually one larva is found/root, and up to 50% of larvae are parasitised by the fly, *Bithia modesta* (Meigen) (Diptera: Tachinidae).

The insect is widely dispersed in the northern Mediterranean and north-western European countries except Scandinavia. Percent infestation of plants varies considerably with location. However, an important part of mortality of plants more than 1-yr-old seems to be due to this insect, although regrowth and seed production of plants infected in the laboratory does occur. This aspect is currently being examined in laboratory and field experiments.

Host-specificity tests of the first instar larvae were made using insects from three widely separated sources; *R. crispus* from Rome, *R. pulcher* from Montpellier, France, and *R. pulcher* from three sites in central Portugal. Adults from these sites were mated, the eggs stored and newly hatched larvae were transferred onto stems of test plants. Five larvae for each of five test plants were used. Controls were the same number of larvae placed onto *Rumex* plants. Sixty-four test plants were selected for their taxonomic relationship to *Rumex* or for their agricultural importance to Australia. The plants were dissected after 2 wks, which is sufficient time for larvae to reach the third instar, and hence have initiated attack on the plant. This testing program is not yet finished, but so far larvae have initiated attack and grown, at least to the second instar, in *Rumex* species from the subgenera *Rumex*, *Acetosella* and *Acetosa*, but not *Platypodium*. Second instar larvae were also found on some plants of *Polygonum* sp. (Polygonaceae), *R. rhabarbarum*, *F. esculentum* and all *E. spinosa*. However, long-term host-specificity tests are needed to see if development can be completed in these plants. *E. spinosa* and *F. esculentum* are annual plants, so possibly would not be available to an insect that attacks its host plant in summer. All other plants not belonging to the Polygonaceae, with the exception of *Persea americana* Miller (Lauraceae), were not attacked. Out of 10 plants of *P. americana*, five exposed to larvae from France and five to larvae from Portugal, two had one second instar larva which had made a tunnel. Further tests over a longer period are needed for this species.

Chamaesphecia doryliformis *(Ochsenheimer) (Lepidoptera: Sesiidae)*

This clearwing moth is found in the western Mediterranean region but not north of mid-Portugal, Spain and Sardinia. Larvae are found in roots of *Rumex* species but the only host in the literature is *R. acetosa* (Rungs 1979). This insect was found commonly in roots of *R. pulcher* in Morocco but rarely in southern Spain and Portugal.

Adults emerge throughout May and June but mostly in May. Its biology and effect on the plant is similar to *B. chrysidiformis*. No host plant specificity testing has been done so far with this species.

Pegomya bicolor *Wied. and* P. nigritarsis *Zett. (Diptera: Anthomyiidae)*

Both *P. bicolor* and *P. nigritarsis* are found as larvae in leaf mines on *Rumex* species in spring and autumn in southern France. There appears to be a number of generations per year. Hennig (1973) lists the host plant records for each species. The chief host plants of *P. bicolor* are *Polygonum* species and *Rumex* species, with doubtful records for *Rheum* species and other Polygonaceae. *Begonia semperflorens* Otto & Link (Begoniaceae) has been recorded as a host plant. The chief host plants of *P. nigritarsis* are *Rumex* species with possibly some attack on other Polygonaceae. Attack on *B. semperflorens* by *P. nigritarsis* needs to be confirmed. Larvae of *Pegomya* species from *Rumex* leaves collected in the Montpellier region will form leaf mines if transferred onto *B. semperflorens* but most die before forming pupae. Further work is needed to distinguish between the larval stages of the two *Pegomya* spp. before any host-specificity testing can be done.

Discussion

No insects were found which are host-specific to *R. pulcher*, and in general the best degree of specificity that could be expected is to the subgenus *Rumex*. This implies that species on native Australian *Rumex* will be exposed to attack. Unfortunately, aside from the taxonomy (Rechinger 1984), nothing is known about the biology of these species, except that some occur as weeds in pastures, while others are rare. It is evident that some attack on Australian native *Rumex* species will have to be accepted if biological control is to be attempted on *R. pulcher*.

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Status of Biological Weed Control in Montana

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Abstract

A total of 22 insect species have been introduced in Montana as biological control agents against nine target weeds since 1948. An additional weed-feeding insect, the tephritid fly, *Urophora quadrifasciata*, introduced in British Columbia, Canada, against *Centaurea maculosa* and *C. diffusa* (spotted and diffuse knapweed) in 1972, has migrated into Montana. Of these 23 insects, five species are well-established, four appear to be established in small numbers, and nine failed to establish. The status of five newly released species has not been determined. Of the established insects, the tephritid fly, *Urophora affinis*, released on *C. maculosa* and the seed-head weevil, *Rhinocyllus conicus*, released on *Carduus nutans* (musk thistle), have shown the fastest increase and dispersal.

État de la Lutte Biologique Contre les Plantes Nuisibles au Montana

Depuis 1948, 22 espèces d'insectes, au total, ont été introduites au Montana pour assurer la lutte biologique contre neuf plantes nuisibles particulières. Un autre insecte se nourrissant de plantes nuisibles, *Urophora quadrifasciata*, introduit en Columbie-Britannique, au Canada, en 1972, a étendu son aire de dispersion jusqu'au Montana. Sur ces 23 insectes, cinq espèces se sont bien établies, quatre espèces semblent s'être établies en petits nombres et neuf espèces n'ont pas réussi à s'établir. Cinq autres espèces d'insectes ont été libérées récemment, mais on ne sait pas encore si elles s'établiront.

Introduction

Although the concept of biological weed control is fairly new in Montana, the use of natural enemies to control weeds has been in practice for some time, dating back to the release of two defoliating beetles, *Chrysolina quadrigemina* (Suffrian) and *C. hyperici* Forster (Coleoptera: Chrysomelidae) on St. Johnswort, *Hypericum perforatum* L. (Clusiaceae), in 1948 (Roemhild 1956). However, the approach was not taken seriously in the State until the early 1970s when concern over the rapid spread of spotted knapweed, *Centaurea maculosa* Lamarck (Compositae), in western Montana prompted a group of farmers and ranchers to request biocontrol research of the weed by Montana State University. The tremendous public support to the subsequent research effort plus increasing concern over yet another weed, leafy spurge, *Euphorbia esula* L. (Euphorbiaceae), led to the development of a full-time research program of biological weed control by Montana State University in 1976. There are currently two scientists working full-time on the program.

Montana Biocontrol of Weeds Program

A total of 22 insect species have been introduced in Montana as biological control agents against nine exotic weeds of Eurasian origin since 1948. An additional weed-feeding insect, the tephritid fly, *Urophora quadrifasciata* (Meigen) (Diptera: Tephritidae), introduced in British Columbia, Canada, against both spotted and diffuse knapweed, *C. diffusa* Lamarck, in 1972, has migrated into Montana. Of these 23 insects, five species are well-established, four appear to be established in small numbers, and nine failed to establish. The status of five newly released species has not been determined.

There are currently seven rangeland weeds targeted for biocontrol research in Montana, but the emphasis is on three weeds: spotted knapweed, diffuse knapweed, and leafy spurge.

Priority Projects

Spotted and diffuse knapweed. Spotted knapweed is the fastest spreading rangeland weed in Montana, currently infesting approximately 8,000,000 ha (2 million acres) (French and Lacey 1983). The majority of the infestation occurs west of the Continental Divide but it is rapidly spreading eastward (Story and Anderson 1978). The plant is very competitive, due largely to its allelopathic effect on other vegetation. The plant has long been considered a biennial or short-lived perennial, but recent data suggest that the plant commonly lives up to 7 yrs (unpubl. data). The plant reproduces solely by seed.

Diffuse knapweed is very similar to spotted knapweed except it is a biennial and grows on slightly drier sites. Diffuse knapweed is much less abundant than spotted knapweed, infesting an estimated 600 ha (M. Jackson, pers. comm.). Since it is known that many weed workers are mistaking diffuse for spotted knapweed, the actual infestation is probably much greater. The serious threat posed by this weed, combined with the availability of diffuse knapweed-attacking insects already established on spotted knapweed in Montana and in Canada, easily justify efforts against the plant.

A small tephritid fly, *Urophora affinis* Frauenfeld, that attacks flower heads of both spotted and diffuse knapweed, was released at 14 sites in western Montana during 1973–77. Larvae form galls (1 larva/gall) in flower heads, which reduce seed production.

The fly became established, has increased rapidly, and has dispersed to a radius of at least 8 km (5 miles) at all sites. A 4-yr study (1977–81) on its increase and dispersal since release in 1977 at five sites was concluded in 1982. Percent fly-infested seed heads and average number of fly galls/seed head increased significantly at all five sites during the 4-yr period (Story and Nowierski 1984). Percent of fly-infested seed heads in the final year of the study (1981) was 63–99%, and average number of galls/seed head was 2.1–9.3. Up to 24 galls were found in individual seed heads.

Spider predation, an unusually cold winter, and seed head predation by rodents appeared to be the only factors adversely affecting the fly populations. Although winter mortality appears to occur, the fly is capable of surviving the winters of west-central and eastern Montana; large populations of the fly now occur at release sites near Butte, Townsend, Livingston, Geyser, and Roundup, despite extended temperatures of −41°C (−50°F) at some sites during the winter of 1983–84.

Data collected in 1980 showed that fly populations at several release sites were large enough to facilitate large-scale collection and redistribution efforts. Thus, beginning in 1981, public-collection field-days have been held each spring for 4 yrs at a release site near Missoula. Due to tremendous public response, the four field days have resulted in redistribution of an estimated 5 million flies at over 900 spotted-knapweed-infested areas throughout Montana.

U. quadrifasciata, another gall-forming tephritid that attacks the flower heads of spotted and diffuse knapweed, is also established in Montana. This fly, introduced for biocontrol of knapweed at Ned's Creek, British Columbia, Canada, in 1972 (Harris 1980*a*), was found in 1981 to be migrating into western Montana at a rapid rate. Surveys in 1982 and 1983 revealed the fly was established in small numbers throughout much of the knapweed-infested areas of the State.

Although very similar in appearance, the two flies have differences: in contrast to *U. affinis*, which has only one generation/yr, *U. quadrifasciata* normally has two generations/yr, forms thinner galls, and attacks more mature flower heads than *U. affinis* (Harris 1980*a*).

U. quadrifasciata is spreading noticeably faster than *U. affinis*, even though the latter insect is well-established in both British Columbia and Montana. The faster spread of *U. quadrifasciata* is probably due to the fly's two-generation/yr seasonal cycle, but it could also be a behavioral trait.

Of special interest are complementary effects of the two flies on spotted knapweed. Since they attack flower buds at different plant growth stages, those immature flower buds escaping attack by *U. affinis* are attacked later by *U. quadrifasciata*. As a result, the most significant spotted knapweed seed reductions are probably occurring where the two fly species coexist. Preliminary data in 1983 showed that seed reductions of approximately 60% occurred at one site in Montana where a high density of *U. affinis* was associated with a low density of *U. quadrifasciata* (unpubl. data). In British Columbia, where both fly species are well-established, spotted knapweed seed reductions of 95% have been reported (Harris 1980*b*).

A third insect released on the knapweed project is the moth, *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae), whose larvae feed on florets and seeds of spotted knapweed. Four releases of this moth were made in western Montana during 1980–83. Seed head data collected in 1982 yielded an 11.2% infestation in a field cage compared to only 1.0% at a field-release area. However, no viable moth larvae were found in seed heads sampled at all sites in May 1984, following the unusually cold winter of 1983–84. Although attempts to re-establish the moth in field cages are underway, it appears the moth may be better suited for release in the warmer climates of Idaho, Oregon, and Washington.

The two seed-head-fly species can significantly reduce seed production. Thus, a study was initiated in 1983 to evaluate the extent of competitive interference between the moth and the two fly species, since all three insects attack the flower heads. First-year data (1983) showed that the moth larvae did compete with larvae of *Urophora* spp. The moth larvae burrowed into the hard galls of *U. affinis* and killed the fly larvae in up to 30% of moth-fly-infested seed heads. The moth's effect on *U. quadrifasciata* was not determined.

Despite this competition, the combined presence of the three insects significantly reduced seed production in attacked seed heads below the level caused by the two fly species alone ($P < 0.05$). Mean number of seeds/seed head ($\pm SE$) collected randomly within field cages containing only the two fly species versus cages containing both the moth and the two fly species was 7.59 ± 0.91 and 5.73 ± 0.45, respectively (unpubl. data). Although the moth has an obvious impact on spotted knapweed seed production, further assessment of its compatibility with the two fly species is needed before further releases are made. The moth probably only affects seed production in attacked seed heads, while the fly galls affect seed production on the entire plant (Harris 1980*b*). Thus, potential for reduced seed production caused by a large moth population must be weighed against possible increased seed production caused by the moth's destruction of fly galls. A fourth knapweed insect released in Montana is a beetle, *Sphenoptera jugoslavica* Obenb. (Coleoptera: Buprestidae), that mines roots of diffuse knapweed. Small numbers of the beetle were released in 1983 near Superior; status of the beetle has not yet been determined.

Small numbers of *Agapeta zoegana* (L.) (Lepidoptera: Cochylidae) and *Pelochrista medullana* Stgr. (Lepidoptera: Tortricidae), two root-mining moths that attack both spotted and diffuse knapweed, were released near Stevensville in July 1984. The insects were collected in Europe by the Commonwealth Institute of Biological Control (CIBC) in Delemont, Switzerland, under contract with Montana State University. Status of the two insects is not yet known.

Leafy spurge. Leafy spurge is the rangeland weed causing the greatest concern on a statewide basis. This perennial plant is very competitive, very persistent, and is extremely difficult to control with herbicides. Statewide in distribution, the plant infests an estimated 200,000 ha (500,000 acres). The plant reproduces both by seed and rhizomatous roots.

A defoliating moth, *Hyles euphorbiae* L. (Lepidoptera: Sphingidae), was released at numerous sites in Montana in 1966 and 1973 (Story 1979). Since, by 1981, no moths had been recovered, the moth was considered a failure. However, in 1982, 9 yrs after release, *c.* 100 larvae were found at a release site near Bozeman, Montana. Several thousand larvae were found at the same site in 1984 (N. Rees, pers. comm.). Small number of *Hyles* larvae were also found at a release site near Missoula in 1983 and 1984. In view of the insect's obvious establishment in Montana, work with this insect has been renewed. Rearing efforts at both Corvallis and Bozeman resulted in the release of *c.* 1000 *Hyles* in Montana, while 300 *Hyles* were sent to North Dakota for release.

Small numbers of the root-mining beetle, *Oberea erythrocephala* (Schrank) (Coleoptera: Cerambycidae), were released on leafy spurge at three sites in 1982 and 1983. Adults successfully emerged in 1984 (1 yr after release) at a release site near Columbus (N. Rees, pers. comm.). The status of the insect at two other sites is not known.

A root-mining moth, *Chamaesphecia tenthridiniformis* (Schiff.) (Lepidoptera: Aegeriidae), released in 1977, failed to establish.

Other Projects

Although current emphasis is on the three above-mentioned weeds, some work is also being done on four other weeds: musk thistle (*Carduus nutans* L.; Compositae); Dalmation toadflax (*Linaria dalmatica* [L.] Mill.; Scrophulariaceae); Canada thistle (*Cirsium arvense* [L.] Scop.; Compositae); and St. Johnswort (*H. perforatum*).

Musk thistle. Musk thistle is a problem in many areas of western Montana where it forms heavy infestations that reduce pasture utilization. The plant is a biennial and reproduces solely by seed.

Two insects, a seed-head weevil, *Rhinocyllus conicus* Froelich, and a crown weevil, *Trichosirocalus horridus* (Panzer) (both Coleoptera: Curculionidae), have been released on musk thistle. *R. conicus*, first released near Bozeman in 1969, became established over a 1280 km^2 area within 5 yrs (Hodgson and Rees 1976). Due to numerous redistribution efforts, the weevil is now established at nearly all musk-thistle-infested areas of the State. Rees (1977) reported that the weevil appeared to be reducing musk thistle seedling density. The other weevil, *T. horridus*, released in 1978–81 at several sites near Corvallis, failed to establish.

Dalmation toadflax. Dalmation toadflax is a serious problem in extreme western Montana where an estimated 16,000 ha (40,000 acres) of rangeland are infested with the plant. The plant is very aggressive, very persistent, and is difficult to control with herbicides.

A defoliating moth, *Calophasia lunula* (Hufnagel) (Lepidoptera: Noctuidae) was released near Whitehall and Yellowstone National Park in 1972 and 1975, respectively, but failed to establish (Story 1979). Efforts in 1984 to mass-rear the moth resulted in release of *c.* 1100 larvae at sites near Plains and Missoula, and shipment of 500 larvae to Oregon. The status of these new releases has not been determined.

Canada thistle. Canada thistle is a statewide problem, infesting an estimated 280,000 ha (700,000 acres) of crop-, pasture-, and rangeland. Three insects have been released on Canada thistle: a stem-mining weevil, *Ceutorhynchus litura* (F.) (Coleoptera: Curculionidae), a stem-gall tephritid fly, *Urophora cardui* (L.), and a defoliating beetle, *Altica carduorum* Guérin-Méneville (Coleoptera: Chrysomelidae).

C. litura, released near Bozeman in 1973, became well-established but, by 1978, had dispersed only 203 m from the release point. Recently, however, the weevil has begun to disperse much faster and can now be found out to 3.2 km (2 miles) (N. Rees, pers. comm.). Redistribution of *C. litura* larvae in 1979 resulted in its establishment at sites near Corvallis and Plains, in western Montana.

U. cardui was released at three sites near Corvallis during 1978–82. The fly failed to establish at two open, relatively dry sites, but appears to be established in small numbers at a low, moist, and well-protected site.

A. carduorum, released at several sites in western Montana in 1966, failed to establish.

St. Johnswort. St. Johnswort is a localized problem in rangeland and forests of western Montana. The first attempt to control a weed with insects in Montana occurred against this plant in 1948 when two defoliating chrysomelid beetles, *C. quadrigemina* and *C. hyperici*, were released at several sites in western Montana (Roemhild 1956). *C. quadrigemina* became established and has dispersed throughout most of the St. Johnswort-infested areas of the State but has had no noticeable effect on St. Johnswort density. *C. hyperici* was initially recovered in small numbers but its present status is not known. The status of the leaf-gall fly, *Zeuxidiplosis giardi* Kieffer (Diptera: Cecidomyiidae) released near Bozeman in 1983 is not known. *Agrilus hyperici* (Cr.) (Coleoptera: Buprestidae), a root-boring beetle released in 1955 and 1976, failed to establish.

Terminated Projects

Two root and stem weevils, *Microlarinus lareynii* (Jacquelin duVal) and *M. lypriformis* (Wollaston) (Coleoptera: Curculionidae), released in 1963 (Maddox 1976) on puncturevine (*Tribulus terrestris* L.; Zygophyllaceae) near Billings, and two moths, *Coleophora parthenica* Meyrick and *C. klimeschiella* Toll (Lepidoptera: Coleophoridae), released on Russian thistle (*Salsola iberica* Sennen & Pau; Chenopodiaceae) in 1979 and 1981–82, respectively, in central Montana failed to establish. No further work with these two weeds is planned.

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Biological Control of Harrisia Cactus, *Eriocereus martinii*, in Central Queensland by the Mealybug, *Hypogeococcus festerianus*, Nine Years After Release

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Abstract

Harrisia cactus, *Eriocereus martini*, is a major weed in central Queensland. A mealybug from Argentina, *Hypogeococcus festerianus*, first released in 1975, showed early promise and has been spread widely throughout the range of the plant reducing cactus cover from 50% to < 1%. A slight resurgence varying seasonally is now occurring. The present situation is discussed.

Lutte Biologique Entre le Cactus du Genre Harrisia, *Eriocereus martinii*, au Centre du Queensland au Moyen de la Cochenille *Hypogeococcus festerianus* Neuf Ans Après son Introduction

Le cactus *Eriocereus martinii* est une des principales plantes nuisibles du centre du Queensland. Une cochenille d'Argentine, *Hypogeococcus festerianus*, semblait d'abord prometteuse au moment de sa première introduction en 1975 et elle a été vastement disséminée dans toute l'aire de distribution de la plante, réduisant ainsi la proportion du couvert végétal occupé par ce cactus de 50% à moins de 1%. À l'heure actuelle, il y a de légères réapparitions saisonnières du cactus. Le rapport traite de la situation présente.

Introduction

Harrisia cactus, *Eriocereus martinii* Lab. (Cactaceae), is a major weed of rangelands in central Queensland, with infestations present over an area of 3×10^6 ha (McFadyen and Tomley 1978) (Fig. 1).

A mealybug, *Hypogeococcus festerianus* (Lizer y Trelles) (Hemiptera: Pseudococcidae), first released in 1975, established readily and after showing early promise, became the basis of a biological control programme which superseded chemical and mechanical control methods in 1979 (McFadyen and Tomley 1981*a*). This programme has been continued with large-scale releases of field-collected mealybugs over most of the area infested, and successful biological control is considered to have been achieved (McFadyen and Tomley 1981*b*). It is now nine years since mealybugs were first released. Detailed measurements of the ground covered by cactus and the number and size of the plants remaining are a guide to what is happening.

Three separate study sites are maintained. In the early stages (1975–78), a stem-borer, *Alcidion cereicola* Fisher (Coleoptera: Cerambycidae), which destroys the woody stem tissue, was also involved, but is no longer present because it requires older stems which are not now available.

Evaluation Methods

Initially plant cover at the three sites was measured by setting out 10 fixed-line transects 20 m long in each study area (McFadyen and Tomley 1981*a*) and these measurements of percent cover were adequate to show changes in the plant population while cover exceeded 10%.

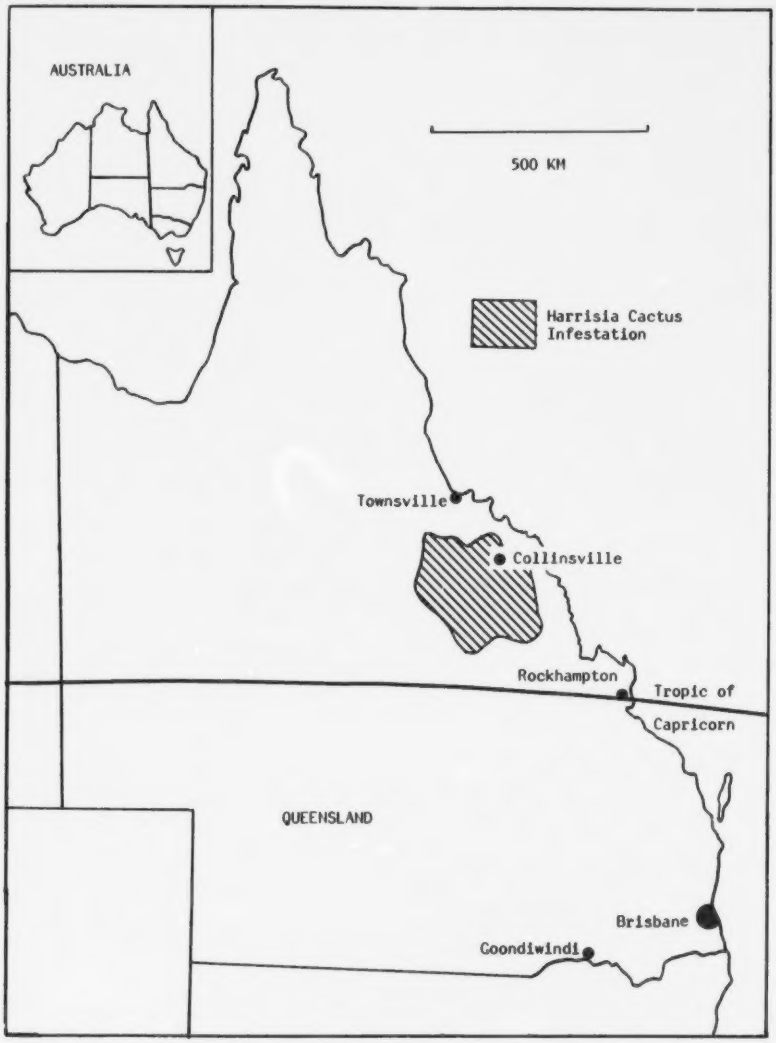
AUSTRALIA
500 KM
Harrisia Cactus Infestation
Townsville
Collinsville
Rockhampton
Tropic of Capricorn
QUEENSLAND
Brisbane
Goondiwindi

Fig. 1. Main area of Harrisia cactus (*Eriocereus martinii* Lab.) in Queensland.

After 3–4 yrs, the mealybugs had reduced the ground covered by cactus to < 10% (Fig. 2). Permanent 10 × 10 m quadrats were set out using the original transects as baselines, and the number and size of plants in the quadrats was also recorded.

Measurements of Harrisia cactus growth rates were not made in the Collinsville area prior to release of the insects, and no suitable site free from insect attack is now available. However since 1978 measurements of cactus density have been made at Goondiwindi in southern Queensland in areas free of mealybug.

As counts of mealybug are not practicable, only their presence or absence on plants was recorded.

Results and Discussion

At the experimental sites, the dramatic and continued reduction in percent ground covered by Harrisia cactus is shown in Fig. 2. Fig. 3 shows cactus populations as plants ha^{-1} and starts when percent cover was reduced below 10%. Site A lags about 3 yrs behind the other two sites because the mealybugs reached the area by natural spread in 1978, 3 yrs after they were released at the other sites.

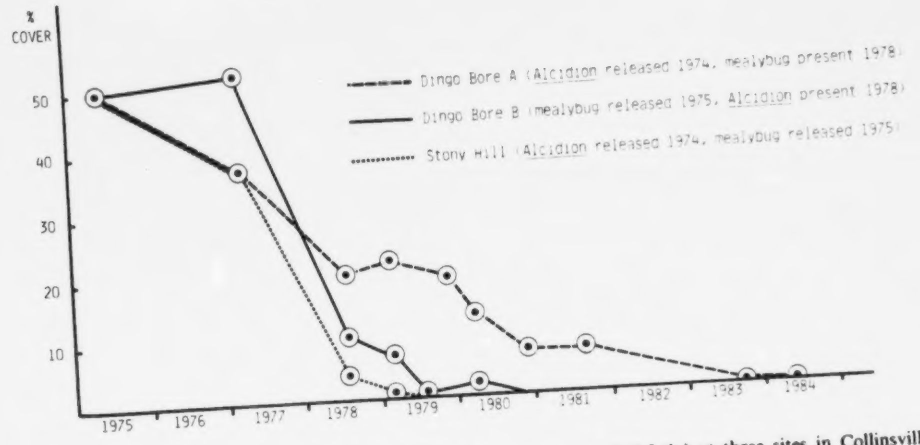

Fig. 2. Changes in percent cover by Harrisia cactus (*Eriocereus martinii* Lab.) at three sites in Collinsville, Qld.

Since 1979, when use of chemical sprays was abandoned in favour of large-scale spreading of the mealybug, infestations of cactus affecting thousands of ha have been successfully controlled by the mealybug, with cactus populations reduced to a very low level. However, very dry conditions since 1980 have reduced mealybug survival and possibly affected results. Harrisia cactus plants have a well-developed underground tuber system, which in suitable conditions readily produces new stems if top growth is removed. Normally, continued feeding by mealybugs on new stems destroys the tuber system by draining all reserves. However, in dry conditions regrowth from tubers is reduced or delayed, and in the absence of living stems, the mealybug may die out locally before all tubers have been completely killed. When rain does fall, small shoots grow up from the remaining tubers, and these may be free of mealybug. In May 1984, at Site B, mealybug was present on only 1 plant out of 158 in a total area of 0.1 ha, while at Site A, the majority of the 161 plants in the 0.1 ha area had mealybug still present.

Very few seedlings are now found at the study sites; new growth is almost entirely from tubers. Seed viability of Harrisia cactus is very low after 4–5 yrs (G. Diatloff, pers. comm.) and field observations showed that very few fruits were produced in the study areas since 1977–79.

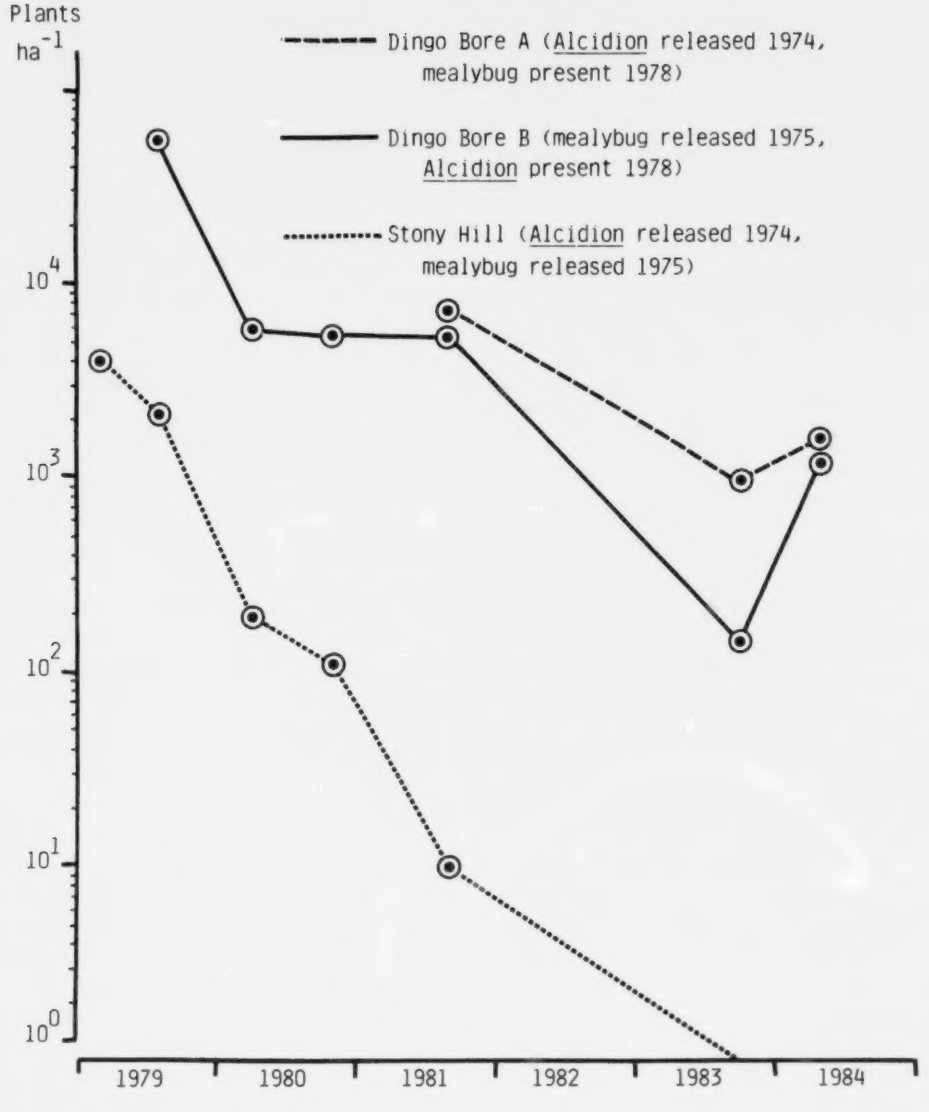

Fig. 3. Reduction in Harrisia cactus (*Eriocereus martinii* Lab.) plant density at three sites in Collinsville, Qld.

At the plant densities now found, death of small plants from causes other than insects (e.g. dehydration, trampling, marsupial feeding), is becoming increasingly significant as described by Crawley (1983). As a result, seasonal variation which was previously ignored, has become significant. In autumn (March–May) after summer rains, there may be numerous small plants and shoots, most of which will not survive the dry winter and spring, and thus would not be present in early summer. Extent and duration of this seasonal variation will have to be taken into account in future. Results from

Goondiwindi (Fig. 4) show that even without mealybug attack, annual increase in cactus density is very variable, and may even be negative in dry years. Monitoring progress of a biocontrol agent in such a plant must therefore be a long-term project.

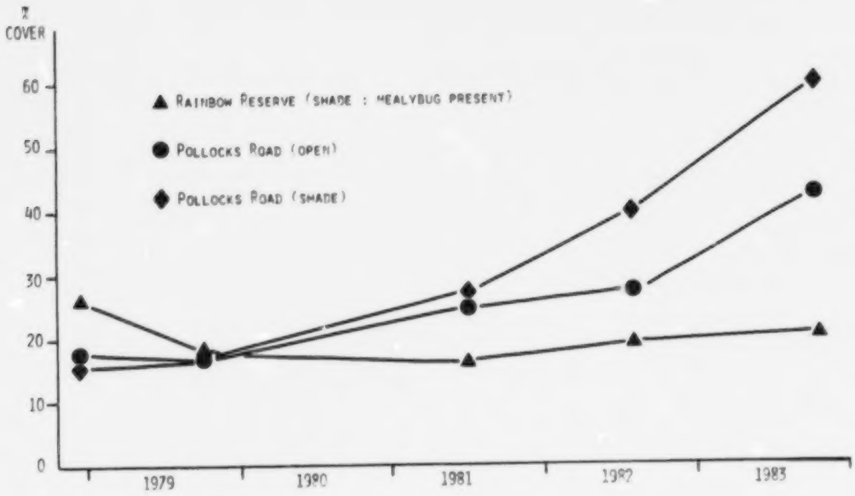

Fig. 4. Changes in percent cover by Harrisia cactus (*Eriocereus martinii* Lab.) at three sites at Goondiwindi, Qld.

Conclusions

Though after 9 yrs an equilibrium level has still not been reached, indications are that final plant density will be very low, such that it no longer interferes with rangeland grazing. Occasional re-distribution of mealybug colonies should be the only control measure required.

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The Biological Control of *Acacia nilotica indica* in Australia

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Abstract

Acacia nilotica indica, originally introduced as a beneficial shade tree, has become a serious weed in northern Queensland, particularly in the arid sheep- and cattle-grazing regions. It forms dense prickly thickets which interfere with stock mustering. A biological control programme was commenced in 1981 and to date, four insect species have been imported into Queensland. The seed-feeding bruchid, *Bruchidius sahlbergi*, has become established and the present status of this insect and the recently released green-shoot-boring gracillariid, *Cuphodes profluens*, is discussed.

De Lutte Biological Contre *Acacia nilotica indica* en Australie

Acacia nilotica indica qui, à l'origine, a été introduite comme essence d'ombre bénéfique, est actuellement une plante nuisible qui cause de graves problèmes dans le nord de la zone tropicale de Queensland, particulièrement dans les régions semi-arides de pâturages des moutons et du bétail où cette espèce forme de denses fourrés épineux qui nuisent au rassemblement du bétail. Un programme de lutte biologique a été mis en oeuvre en 1981 et, jusqu'à présent, deux espèces d'insectes ont été mises en liberté à Queensland. Un bruche granivore *Bruchidius sahlbergi* s'est établi dans ces régions, et le rôle actuel de cet insecte ainsi que celui du gracilariidé perceur de pousses vertes *Cuphodes profluens* qui a récemment été introduit font l'objet du présent document.

Introduction

Origin and Distribution of Acacia nilotica *(L.) Delile spp.* indica *(Benth.) Brenan (Mimosaceae)*

A. nilotica indica is a prickly shrub or spreading tree which grows to about 7.5 m high and can grow into dense thickets (Kleinschmidt and Johnson 1977). It is one of about nine subspecies of the *A. nilotica* complex formerly known as *A. arabica* (Lam.) Willd. This complex is native to Africa and the Indian sub-continent (Brenan 1957; Ali and Faruqi 1969). *A. nilotica indica* is native to India and Pakistan (Ali and Faruqi 1969). It probably occurs in Iraq (Townsend 1968); it occurs in Tanzania but was probably introduced there (Brenan 1959). It was introduced into Australia early this century and is restricted to the State of Queensland where it is known as prickly acacia. A few trees have been recorded in the Northern Territory adjacent to the Queensland border (I.L. Miller, pers. comm.).

A. nilotica indica *in Queensland*

A. nilotica indica has been used as a shade tree in tropical areas of Queensland since its introduction. Pollock (1926) noted it growing extensively in two coastal areas —

Bowen and Rockhampton (Fig. 1). He recommended the tree to sheep graziers as filling a need for a shade tree in western Queensland. He warned however, that when consumed by cattle 'the seeds are not masticated and pass whole through the digestive track thus causing numbers of young trees to appear where they are not wanted'. The weed potential of this plant was thus forecast before its use on the plains of western Queensland.

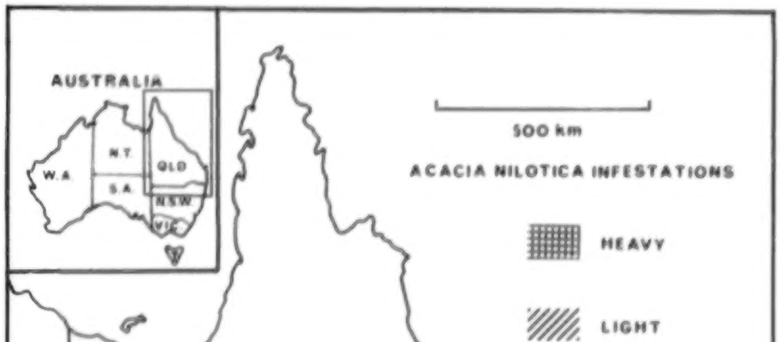
AUSTRALIA
W.A.
N.T.
QLD
S.A.
NSW
VIC
500 km
ACACIA NILOTICA INFESTATIONS
HEAVY
LIGHT
Townsville
Richmond
Bowen
Hughenden
N.T.
Winton
Rockhampton
Tropic of Capricorn
Longreach
QUEENSLAND
SOUTH AUSTRALIA
Brisbane
600mm
750 mm
NEW SOUTH WALES

Fig. 1. Areas of infestation of *Acacia nilotica* (L.) Delile *indica* (Benth.) Brenan in Australia.

During the 1930s, '40s and '50s the plant was grown extensively around homesteads, artesian bore tanks and drains in arid areas of tropical northern Queensland where its shade was claimed to be extremely beneficial in improving lambing rates and fleece quality. No other tree species will grow on the brown, self-mulching, cracking clay soil plains and it is not surprising that *A. nilotica indica* has been grown so enthusiastically not only for its shade, but also for the high nutritive value of its leaves and pods which are relished by sheep. Brunnich (1926) reported these pods to have a protein content of 12.5% and many graziers claim that pods helped their flocks survive recurrent drought conditions.

It was not until a decline in the wool industry in the late 1950s when many sheep-grazing properties converted either wholly or partly to cattle-grazing that the tree's potential for weediness became fact. In favourable seasons, the seeds spread over large areas by cattle germinated and grew into impenetrable prickly thickets. Harvey (1981) has shown by feeding trials with sheep and cattle that the greatly increased survival of seed ingested by cattle would at least partly explain the upsurge in growth of prickly acacia.

A. nilotica was declared a noxious plant in 1959. Its declaration was mooted in 1951, but this was shelved as many graziers were still convinced that they could manage it successfully. Even now it is generally agreed by landholders that maintenance of large shade trees around properties would be very desirable if control over its spread could be achieved.

An accurate assessment of the total area infested with prickly acacia is difficult to obtain. An attempt using questionnaires was made in 1979 by P. James (pers. comm.). Information obtained by James indicated that 5000–6000 km^2 of prime grazing land was infested to some degree by prickly acacia. Up to 20% of that infestation was regarded as impenetrable. One property of 20,000 ha near Richmond was estimated to contain 6000 ha of impenetrable thickets, 8000 ha of heavy infestation and 4000 ha of scattered prickly acacia. This property had four prickly acacia trees in 1960. Another property of 20,000 ha near Richmond was 100% infested with 8000 ha of impenetrable thickets, 4000 ha heavy infestation and 8000 ha scattered plants.

Since 1979, the situation has continued to worsen at an alarming rate with much of the scattered and heavy infestations becoming impenetrable. If this plant is not controlled, the arid grasslands of northern Queensland will be lost to the pastoral industry. Areas of infestation are shown in Fig. 1.

Biological Control of A. nilotica indica

The weed has now become too widespread to be cheaply controlled either mechanically or by the use of herbicides, and biological control is being attempted.

Following field surveys in Pakistan by Mohyuddin (1981), the Commonwealth Institute of Biological Control was contracted by the Queensland Government through the Stock Routes and Rural Lands Protection Board to conduct a programme of exploration and evaluation of likely biological control agents. Particular attention was paid to those agents likely to interfere with the plant's reproduction either by the prevention of flowering or by flower or seed destruction.

As the host-specificity testing involved many plant species not readily available in Pakistan, the testing of all candidates was finalized under quarantine in Australia.

Four insect species have been received in Australia to date; of these, *Bruchidius sahlbergi* (Schilsky) (Coleoptera: Bruchidae) and *Cuphodes profluens* Meyrick (Lepidoptera: Gracillariidae) have been field-released; *Tephrina disputaria* Gn. (Lepidoptera: Geometridae) was rejected because of host-specificity doubts; and *Ascalenia callynella* Kasy (Lepidoptera: Momphidae) is undergoing final host testing.

Results and Discussion

Bruchidius sahlbergi

This seed-boring beetle is widespread in Pakistan (Mohyuddin 1981). It oviposits into the crevice of partially dehisced pods and on hatching, the larva moves from one seed chamber to another to find an unattacked seed. One larva will effectively destroy one seed and multiple larval feeding within a seed is rare. The larva enters the seed using the pod wall for leverage and it is doubtful if larvae can attack seed once it has fallen from the pod.

Approximately 1000 beetles were imported into Queensland in four shipments in the period from November 1981 to January 1982. Field liberations were commenced in Bowen in August 1982 after additional testing under quarantine confirmed their specificity to prickly acacia. In the following 18 months, approximately 309,000 beetles were released at 96 sites. Eighty-one of these sites were located in the arid region of Queensland with an annual rainfall of < 750 mm; the remainder were located in higher-rainfall coastal regions. All prickly acacia growing in the arid region had been under severe drought stress from before the previous flowering period, with the consequence that only trees growing around permanent water such as artesian bore drains produced a seed crop in November–December 1982. These areas offering both shade and water were stock camps and as pods fell, they were eagerly consumed.

To ensure availability of seed in the 1983/84 season, all liberations in this region were made near permanent water. Beetles were released into unstocked areas wherever possible; alternatively, pods were raked into heaps and protected from stock with fallen timber.

B. sahlbergi has readily established at 80% of the release sites. Those sites where the beetles have failed have been either destroyed by floods in May and December 1983 or eaten by stock. At many sites, their continued survival is threatened by a shortage of suitable seed, but wherever stock has been excluded, establishment appears assured. Fifty-two percent of seed from the 1983/84 crop was attacked by *B. sahlbergi* at one Winton site four months after its fall. A further 30% was destroyed at this site by the cosmopolitan *Caryedon serratus* (Oliver) (Coleoptera: Bruchidae).

Cuphodes profluens

Larvae of this small moth tunnel in young, green shoots of prickly acacia. Following initial host-specificity testing by Siddique *et al.* (1982), five shipments totalling 1299 pupae were sent to Australia in 1983. From these, 739 live moths were obtained. On successful completion of host testing under quarantine in Australia, field liberation was commenced in November 1983. To date, 3395 moths have been released at 14 sites. Insufficient time has elapsed to determine establishment.

It is hoped that this insect will attack sufficient young tips to make a significant reduction in number of inflorescences produced.

Tephrina disputaria

This small moth is the most abundant and widespread defoliator of *A. nilotica indica* occurring throughout Pakistan (Mohyuddin 1981). Initial testing in Pakistan indicated that it was probably host-specific. Subsequent testing showed that its larvae could complete their development on *A. deanei* (R.T. Baker) Welch in Australia and on *A. hydaspica* J.R. Drumm. *ex* R. Parker in Pakistan. The adult oviposits indiscriminately when caged and as it was impossible to prove host-specificity, this insect was not accepted as a control agent for release in Australia.

Ascalenia callynella

This green-shoot-borer has only recently been received into quarantine in Australia and as yet, final host-specificity testing has not concluded. As with *C. profluens*, the aim of this introduction is to reduce flowering of prickly acacia by destruction of flower-bearing tips. Siddiqui and Mohyuddin (1984) reported that in Pakistan unattacked shoots had a significantly higher number of inflorescences than those attacked by *A. callynella*.

Acknowledgments

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Bruchid Seed Beetles for Control of *Parkinsonia aculeata* in Australia

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Abstract

Parkinsonia aculeata, is a spiny, leguminous tree that is a weed in northern Australia. It blocks access to waterholes, shades out desirable vegetation, and makes mustering of cattle difficult. The bark of *P. aculeata* can photosynthesize and as the plant can resprout from dormant buds if the stem is damaged, it may be difficult to control by leaf- or stem-feeding insects. In the New World *P. aculeata* is attacked by five species of bruchid seed beetle (Coleoptera: Bruchidae). Of these five, three species appear to have potential as control agents of *P. aculeata* in Australia. *Penthobruchus germaini* has only been collected from *P. aculeata*. *Mimosestes ulkei* only attacks the closely related genera of *Parkinsonia* and *Cercidium* in the field. Although *Mimosestes amicus* attacks four plant genera, two are *Parkinsonia* and *Cercidium*, one is *Prosopis* (not native and considered weedy in Australia), and the last genus, *Acacia*, is not an important host. The possibilities of introducing these species into Australia and their potential for controlling *P. aculeata* is discussed.

Utilisation des Bruches dans la Lutte Biologique Contre *Parkinsonia aculeata* en Australie

Parkinsonia aculeata est un arbre légumineux épineux qui est une plante nuisible dans le nord de l'Australie. Elle empêche l'accès aux nappes d'eau, ombrage la végétation utile et nuit au rassemblement du bétail. L'écorce de *P. aculeata* est photosynthétique et, étant donné que la plante possède des bourgeons sensibles qui sont activés lorsque la tige est endommagée, la lutte biologique au moyen d'insectes qui mangent les feuilles ou la tige peut être difficile. Dans le nouveau-monde, *P. aculeata* est ravagé par cinq espèces de bruches (Coléoptères: Bruchidés). Parmi les cinq bruches, trois semblent prometteurs comme agents de lutte biologique contre *P. aculeata* en Australie. *Penthobruchus germaini* n'a été relevé que sur *Parkinsonia aculeata*. *Mimosestes ulkei* n'infeste que les deux genre étroitement apparentés, *Parkinsonia* et *Cercidium*, dans les champs. Bien que *M. amicus* possède quatre genres-hôtes, deux sont *Parkinsonia* et *Cercidium*, un est *Prosopis*, soit une plante nuisible non indigène en Australie et, finalement, un *Acacia*, qui n'est pas un hôte important. L'auteur étudie s'il est possible d'introduire ces espèces en Australie et si elles peuvent servir dans la lutte contre *P. aculeata*.

Introduction

Parkinsonia aculeata L. (Leguminosae: subfamily Caesalpinioideae) is a small (to 10 m), spiny, leguminous tree which has many common names including Retama, Mexican Palo Verde, and Jerusalem Thorn. It is thought to be native to tropical America but has been spread throughout the world as an ornamental and shade tree.

The caesalpinioid legumes include no species of wide agricultural importance but are highly valued as ornamentals; e.g. *Bauhinia*, *Caesalpinia*, *Cassia*, and *Delonix* (Isley 1975). Australian species of *Cassia* are an important component of the native Australian flora, as well as being increasingly cultivated as ornamentals.

The genus *Cercidium* is very closely related to *Parkinsonia* and putative hybrids have been found in the field (Carter 1974). There has been longstanding and continuing debate as to whether *Cercidium* is a valid genus, or should be included in *Parkinsonia*. Brenan (1963) decided that there was no reason for maintaining *Cercidium* as a distinct genus from *Parkinsonia*, while Carter (1974) supported the validity of *Cercidium*, and Isley (1975) wrote 'the differences amongst the constituent spp. of *Parkinsonia* are not significantly great to merit generic segregation'. Polhill and Vidal (1981) concluded 'whether *Cercidium* is included in *Parkinsonia* (Brenan 1963) or excluded (Carter 1974) depends essentially on whether focus is made on the early radiation or on the secondary radiation responsible for the *Cercidium* core'.

In northern Australia *P. aculeata* is a troublesome weed. It grows in dense thickets beside rivers and dams and its sharp spines make mustering of cattle difficult and dangerous. These thickets prevent stock from gaining access to waterholes and shade out desirable vegetation (Miller and Pickering 1980). Areas where it is pestiferous are often remote and inaccessible and although it can be controlled chemically, this is difficult and costs are prohibitive. Mechanical control is seldom completely effective, with regrowth of suckers and germination of seed causing reinfestation. Biological control appears to be the only feasible alternative.

P. aculeata may be a difficult candidate for control by leaf- and stem-feeding insects. During much of the year the plant is without leaflets, and photosynthesis is carried out by the tough, flattened leaf rachis and by the green stem. If the stem is damaged the plant will regenerate from dormant buds at, or near ground level. These suckers can grow up to 250 cm in six months.

Insects that attack the seed appear to offer the best prospect for biological control. Five species of bruchid seed beetle (Coleoptera: Bruchidae) attack *P. aculeata* in the New World. Three of these species, *Mimosestes ulkei* (Horn), *M. amicus* (Horn), and *Penthobruchus germaini* (Pic), have potential as control agents. Of the other two, *S. limbatus* (Horn) is the extreme example of a generalist, attacking 39 species in eight genera (Johnson 1981*a*), while *Mimosestes mimosae* (Fabricius) is primarily an *Acacia* bruchid, attacking six species of *Acacia*, as well as *Parkinsonia*, *Caesalpinia*, and *Ceratonia* (Kingsolver and Johnson 1978).

Materials and Methods

Pods of *P. aculeata* were collected in Texas and Arizona in 1983 and 1984 and held for adult emergence in 500 ml paper cups with plastic lids.

Many pods of *P. aculeata* with a low incidence of bruchid damage were collected from trees at Temple, Texas, in November 1983. Undamaged pods were selected and placed in two 500 ml wide-mouth fruit jars, 30 unsexed adults of *M. ulkei* were added to each jar, and the jars incubated at 30°C. One container of pods, before addition of bruchids, was heated to 50°C overnight to kill any bruchid larvae that might be present. The two containers were sampled monthly until August 1984 and *M. ulkei* adults counted and removed from the containers. On 5 August 1984, 20 pods from each container were dissected and examined for presence of bruchid eggs and seed damage. Thirty damaged, and thirty seeds from which *M. ulkei* had emerged were weighed.

Seeds of *P. aculeata* collected from five different sites in south Texas in July 1983 were separated into *M. amicus*-damaged, and undamaged seeds. Ten seeds from which *M. amicus* had emerged and 10 undamaged seeds from each site were weighed, scarified and placed in a germination cabinet at 30°C. Each test unit was 10 seeds on filter paper, in a 100 × 15 mm petri dish with 7.5 ml distilled water added. Percent germination was measured after seven days.

At Brownsville, Texas, on 9 June 1984, 10 green, but almost mature pods were collected from each of five trees of *P. aculeata*. The green seeds were removed from the pods and 10 seeds sampled from each tree. As the seeds were still green, it was possible to dissect them and separate out embryo/cotyledon, endosperm and seed coat. These were air dried at 30°C for two months and then weighed.

In Tucson, Arizona, on 24 July 1984, 25 green, but almost mature pods, 25 maturing pods that were just changing colour from green to brown, and 25 mature pods, were collected and examined for eggs of *M. ulkei* laid on and inside the pods.

Approximately 3000 pods of *Cercidium floridum* Bentham collected at Scottsdale, Arizona, in September 1983, were placed in screw-top fruit jars (500 ml) which had the metal sealing disk removed and paper towelling inserted in its place. The containers were sampled fortnightly between October 1983 and March 1984 and adults of *M. amicus* and *M. ulkei* were removed and counted. Adults of *M. ulkei* used in host-specificity testing emerged from these pods.

In experiment 1, different numbers (in brackets) of mature pods of the following plant species were used: *Gleditsia triacanthos* L. (1); *Tamarindus indica* L. (2); *Caesalpinia pulcherrima* (3); *Acacia wrightii* (5); *Prosopis glandulosa* Torr. (5); *Bauhinia congesta*, immature pods (4); and *P. aculeata* (10). The number of pods used was calculated so that the area of pod of each species was approximately the same. The experiment was replicated three times. Large (18-l) plastic buckets were used as cages. Fifteen *M. ulkei* were added on 9 December and removed on 10 January. At this time pods were separated into species and held in paper cups at ambient laboratory temperature (15–25°C) until 1 May for emergence of the bruchids.

In experiment 2, different numbers of seed (in brackets) of each of the following species — *T. indica* (3), *Phaseolus vulgaris* L. (5), *G. trichanthos* (10), *C. pulcherrima* (10), *P. aculeata* (15), *P. glandulosa* Willd. (20), *C. floridum* (10), *Acacia tortuosa* Willd. (20), *Cassia fistula* L. (10), *Bauhinia purpurea* (5), and *Delonix regia* (Boj.) Raf. (5) — were placed in a petri dish and shaken to distribute. Different numbers of seeds were used so that the total area of seed of each species available to the bruchids was approximately the same (Willson 1982). Seeds were searched under the microscope for entry holes of other bruchids, and 10 unsexed *M. ulkei* were added on 5, 9 and 12 December. On 5 January, the seeds were removed and held by species until 21 March for emergence of adults. On 22 March the seeds were dissected for evidence of any larvae or pupae. The experiment was replicated three times. Replicate 1 was held at 30°C, and replicates 2 and 3 at 15–30°C.

In experiment 3, the seeds of each species were placed in 30 ml plastic cups inside a larger plastic container (26 × 35 × 9 cm), with a gauzed top. Seeds of *C. floridum*, *P. aculeata*, and *D. regia* were used. Five seeds of each species in a cup comprised the test unit and three replicates for each species were used. Thirty unsexed *M. ulkei* were added on 7 February, removed on 16 February, and the temperature maintained at 30°C. Seeds were held in individual cups until 1 May for emergence of adults.

Results

M. amicus emerged from 58 out of 89 (65%) pod collections in Texas and Arizona in 1983 and 1984.

In the culture of *M. ulkei* in *P. aculeata* pods, adults were found at each of the eight sampling dates. In the container that had been heated to 50°C overnight before addition of the bruchids, the 20 pods sampled had 43 eggs (22.75%) laid on the outside of the pod and 146 eggs (77.25%) laid on the inside. Eggs laid inside were either inserted through cracks in the pod wall, laid near *M. ulkei* emergence holes, or laid through small holes (pin-prick size) in the pod surface. The unheated container had three eggs laid on the outside (1.85%) and 159 eggs (98.15%) laid on the inside of the pod. *M. ulkei* adults emerged from 61.90% of heated pods, and from 67.12% of unheated pods. Average weight of damaged seed was 0.074 g and of undamaged seed 0.103 g, a difference of 28.16%.

Average weight of seeds from which *M. amicus* had emerged, collected in S. Texas, was 0.075 g, and of undamaged seeds 0.111 g, a difference of 32.43%. In germination tests, percent germination of scarified, undamaged seeds was 92% and for damaged seeds, 6%.

Green seeds dissected to show weight of different seed parts, yielded an average weight of cotyledon/embryo of 0.024 g, of endosperm 0.030 g, and of seed coat 0.036 g. These were 26.66, 33.33, and 40% of total seed weight, respectively.

Pods sampled at Tucson for *M. ulkei* eggs showed three eggs outside and no eggs inside green pods; one egg outside and two eggs inside just-maturing pods; and two eggs outside and 74 eggs inside mature pods.

From the 3000 pods of *C. floridum* collected in Arizona, 684 adults of *M. ulkei* and 549 adults of *M. amicus* emerged October 1983 to March 1984.

In experiment 1 of the *M. ulkei* host-specificity testing, eggs were laid on all species except *A. wrightii*. Total number of eggs laid on each plant species was: *T. indica* — 1; *B. congesta* —3; *P. glandulosa* — 25; *P. aculeata* — 26; *G. triacanthos* — 31; and *C. pulcherrima* — 37. Two adults of *M. ulkei* had emerged from pods of *P. aculeata* in replicate 2 by 1 May.

In experiment 2, eggs were laid on seeds of all species tested. All seeds except *C. floridum* and *P. vulgaris* were entered by *M. ulkei* larvae. Only one *M. ulkei* emerged, from a seed of *P. glandulosa*. However, dissection of seeds on 21 March showed a live pupa in a seed of *P. glandulosa* and a dead *M. ulkei* adult within a seed of *D. regia*.

In experiment 3, 157 eggs were laid on or around *D. regia* seeds compared to 132 for *C. floridum* and 28 for *P. aculeata*. Seeds of *D. regia* and *C. floridum* were entered by *M. ulkei* larvae, and by 1 May, one *M. ulkei* had emerged from *C. floridum* in replicates 1 and 2. On dissection, one live *M. ulkei* adult was found in a seed of *D. regia*.

Discussion

Mimosestes amicus

M. amicus is a widespread and abundant bruchid (Kingsolver and Johnson 1978) and adults emerged from 65% of *P. aculeata* pod samples I collected in Arizona and Texas. It is a continuous breeder in the laboratory and probably has three or more generations/yr in the field (Swier 1974). Conway (1980) estimated that *M. amicus* destroyed 44.9% of the seed crop of *Cercidium microphyllum* (Torrey) Rose & Johnston in Arizona.

It attacks 11 species of plants in four genera but is probably most common in *Cercidium* (Kingsolver and Johnson 1978). *Prosopis* and *Acacia* spp. are also attacked. Conway (1980) reported it causing an estimated 5% mortality to the seed of *Acacia constricta* Benth.

There are *c.* 660 *Acacia* spp. in Australia (Maslin 1981) and they form a major component of the Australian flora. *Prosopis* spp. are introduced and have become weeds in some parts of the country. A *Prosopis* sp. has invaded 200,000 ha of Western

Australian rangeland, since introduction of a so-called spineless variety in the 1920s (Anon. 1978; Ritchie 1983). *Prosopis* and *Acacia* are in the subfamily Mimosoideae, and this lack of specificity may be a barrier to introduction of *M. amicus* into Australia.

However there is evidence (Evans *et al.* 1977) that seeds of most Australian *Acacia* spp. are very different in chemical composition than seeds of *Acacia* spp. from other parts of the world. Chemical composition of seeds is an important determinant of bruchid specificity (Janzen 1977) and therefore *M. amicus* may not be able to breed in seed of most Australian *Acacia* spp. It is relevant that no *M. amicus* were reared from any of the five species of *Acacia* sampled in Costa Rica (Janzen 1980), while it emerged from 87 and 100% of all *P. aculeata* and *P. velutina* L. samples, respectively.

Another barrier to importation of *M. amicus* is that it will oviposit, and larvae will develop to maturity on green pods (Mitchell 1977). Probably these pods are almost mature and Swier (1974) commented that *M. amicus* would only oviposit on pods with developed cotyledons. Nevertheless there are many problems involved in host-specificity testing with green pods and these may not be easily overcome.

Mimosestes ulkei

M. ulkei is a large, robust bruchid that is easily distinguished from other *Mimosestes* spp. by dark markings on the edge of the elytra. Kingsolver and Johnson (1978) catalogued it as a marginal species outcompeted by *M. amicus* and *S. limbatus*. However, a collection of *C. floridum* pods from Arizona yielded 684 *M. ulkei*, compared to 549 *M. amicus*, which suggests that in certain situations *M. ulkei* may be relatively abundant.

In host-specificity tests, *M. ulkei* was not specific in ovipositional preference, laying eggs on seeds of all species tested, and on pods of all but one species. Adults however only emerged from *P. aculeata*, *C. floridum* and *P. glandulosa*, and one dead and one live adult were found inside seeds of *D. regia* on dissection.

In field collections *P. aculeata* and *C. floridum* are the only verified hosts of *M. ulkei* (Kingsolver and Johnson 1978). These two species are very closely related, and in this instance, *M. ulkei* can be considered to attack across, or within generic lines, depending on which taxonomic view is followed. I have not seen any records reporting *Cercidium* spp. growing in Australia.

M. ulkei developed to maturity in seeds of *P. glandulosa* and *D. regia* but in 3 out of 4 cases, the adults had not emerged by the time the trials were completed. This suggests some factors unfavourable to bruchid development.

As there are no field collections of *M. ulkei* from either *Prosopis* spp. or *D. regia* (Johnson 1981*b*), the barrier to bruchid development may be the pod itself. The legume of *P. aculeata* has a thin, papery wall that offers easy access to bruchid larvae. *P. glandulosa* pods have a leathery outside coat, and seeds are encased inside a hard endocarp within the glutinous pod body. *D. regia* pods are large (up to 50 cm long), and have hard, woody walls, 0.5–1 cm thick. Pods of both species may present a considerable barrier to entry of bruchids not adapted to them.

M. ulkei adults will occasionally lay eggs on green pods but the much preferred site of oviposition is mature pods. Many more eggs are laid within the interior pod cavity than on the pod surface. This may be a mechanism to reduce parasitism or desiccation of the eggs.

M. ulkei appears to breed continuously in the laboratory on mature seeds of *P. aculeata*. In southern Arizona, adults have been observed emerging from mature pods remaining on the tree in April, and have emerged from mature pods collected in

September, and therefore there is the potential for multiple generations of *M. ulkei* to develop in a year.

Although these initial results are promising, further host-specificity testing with both green and mature pods are required before *M. ulkei* could be considered for introduction into Australia. Very large cages may need to be used to give a true idea of ovipositional preference, especially with large pods such as those of *D. regia*. Problems in obtaining pods of different species at the same time, preventing fungal contamination and maintaining seed development, may occur, when testing with green pods.

Penthobruchus germaini

Little is known of the biology of this species, and its potential as a biological control agent of *P. aculeata* is unclear. However it is likely to be specific, as it has only been collected from *P. aculeata* in Argentina and Chile (Kingsolver 1973), and the only two species of *Penthobruchus* are 100% specific to *Parkinsonia* and *Cercidium* within the subfamily Caesalpiniodeae (Johnson 1981*b*).

Potential for Control of P. aculeata *in Australia*

Many authors have reported that bruchids can infest a large percent of host seeds (Southgate 1979). However even in damaged seeds a small percent of seeds may still germinate (Halevy 1974).

Only 6% of seeds from which *M. amicus* adults had emerged germinated compared to 96% germination for undamaged but scarified seeds. It is likely that some of the damaged seeds that germinated would not survive, and growth of seedlings that did would be retarded. Janzen (1976) in artificial damage studies with seeds of *Mucuna andreana*, reported a decline in seedling fitness when only 1% of the seed weight was removed.

M. amicus larvae consumed 32.43% of the seed's weight, while *M. ulkei* larvae ate 29.16%. As the cotyledon/embryo together comprise only 26.66% of the seed's weight, this suggests that most of the cotyledonary tissue, and some of the endosperm was eaten. Observations of damaged seeds confirmed this fact. Janzen (1977) reported that larvae of *Callobruchus maculatus* F. (Coleoptera: Bruchidae) did not grow at all in the polysaccharide rich endosperm of *P. aculeata*.

The seed coat of *P. aculeata* comprised a large 40% of the total weight of the seed. The thickness of this seedcoat is in itself a barrier to bruchid penetration (Janzen 1977), and toxic chemical compounds contained in the seed coat are an additional barrier to bruchid entry (Johnson 1981*a*).

The seed coat of *P. aculeata* is impermeable to water and will not germinate readily unless scarified or chemically treated. Everitt (1983) found that only 1% of untreated 'hard' seed of *P. aculeata* germinated, while there was no change in viability of stored seed after 2 yrs of storage.

In Australia there is probably a large reserve of hard seed already in the soil, and this seed will germinate gradually as the seed coat becomes permeable. This is an important adaption for survival in areas of low and uncertain rainfall, to ensure that the entire seed stock is not destroyed in one false 'break' to the season.

Seeds that have dropped over the years and have been covered by soil remain immune to attack by bruchids. Naked seeds on the surface are also unlikely to be attacked by either *Mimosestes* spp. or *P. germaini*, as these bruchids probably belong to the guild of bruchids that oviposit only on pods. The bruchids that oviposit on scattered seeds on the ground are rare, and are generally in the genus *Stator* (Johnson 1981*c*). Pods on the tree, or mature pods on the ground, before being broken down by weathering, or dispersed by water, are the target for attack by the bruchids considered here.

In Texas, *M. amicus* eggs are attacked by an unidentified egg parasite, while bruchid larvae or pupae in seeds of *P. aculeata* are attacked by three wasp species — *Heterospilus prosopidis, Stenocorse bruchivora,* and *Urosigalpus* sp. (Hymenoptera: Braconidae). Center and Johnson (1976) have reported on the many parasites attacking bruchids in Arizona. Introduction of bruchids without their extensive parasite fauna can only increase the chance of successful biological control.

Compared to the New World, Australia has a poor bruchid fauna (Southgate 1979), and there may be a correspondingly smaller, and perhaps more specialized, number of bruchid parasites than in the Americas. Thus, introduced bruchids may escape the severe depredation from native parasites that has caused considerable high mortality to to some previously introduced biological control agents (Haseler 1981). In Australia, no parasites have yet been found attacking the bruchid, *Bruchidius sahlbergi* (Schilsky), introduced for control of *Acacia nilotica indica* (Benth.) Brenan (Willson, pers. comm.).

Little is known of the ecology of *P. aculeata* populations in Australia, or of the reduction in germination percent that would be required to reduce the population below a self-sustaining level. If one, or all of these bruchid species were introduced into Australia, we know that some seeds would be killed, other seeds would germinate but produce unhealthy seedlings, while others, in which bruchid larvae had entered but died, would germinate more readily than undamaged seeds (Halevy 1974). Unfortunately the total effect of all this on *P. aculeata* populations is impossible to predict, albeit that the potential exists for high levels of infestation to develop, and the level of seed mortality is likely to be far greater than it is at present.

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Chapter Nine
Papers Presented in the Poster Session

Proc. VI Int. Symp. Biol. Contr. Weeds, 19-25 August 1984,
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The Entomological Role of Weeds in Agroecosystems: Implications in Biological Control of Weeds and Insects

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Abstract

Weeds may play important roles in the biology of herbivorous insects and their natural enemies in agroecosystems. Certain weeds for example provide alternate food and/or shelter for natural enemies of insect pests during the crop season but more importantly during the off-season when prey/hosts are unavailable.

Some of these weeds may be subject to biological control programs, and these actions may have several consequences on the set of interactions between crops, weeds and insects in a particular agroecosystem: (1) For example the densities of the particular weed may be reduced to low levels, thus affecting the food supply of specific insect parasites or predators. (2) The introduced weed biocontrol agent may compete with native herbivores of the weed and displace them, thus reducing again the supply of food of natural enemies specific to certain herbivores. (3) On the other hand, the introduced biocontrol agent may serve as alternate food to parasites and predators of insect pests. This could benefit the biocontrol of an insect pest, but would reduce the impact of the introduced herbivore on the weed.

This paper points out some examples of the above conflicts. It also sets a guideline to follow to minimize the possibilities of reducing the overall effectiveness of biocontrol agents against weeds and insects. Biocontrol specialists should have a full appreciation of the multitrophic relationships involved in their particular systems of study. Weed researchers should pay attention to the natural enemy component of their target herbivores, and entomologists in turn should analyze the impact of insect parasites and predators on potential candidate herbivores for biocontrol of weeds.

Effets des Plantes Nuisibles sur les Insectes dans les Agro-Écosystèmes: Conséquences sur la Lutte Biologique Contre les Plantes Nuisibles et les Insectes

Les plantes nuisibles jouent peut-être un rôle important dans la biologie des insectes herbivores et de leurs ennemis naturels dans les agro-écosystèmes. Par exemple, certaines plantes nuisibles constituent une source d'alimentation ou un abri pour les ennemis naturels des insectes nuisibles pendant la saison des récoltes ou, ce qui importe davantage, pendant le saison de pénurie de proies ou d'hôtes.

Certaines de ces plantes nuisibles peuvent être soumises à des programmes de lutte biologique, ce qui peut avoir diverses conséquences sur la série d'interactions entre les récoltes, les plantes nuisibles et les insectes dans un agro-écosystème particulier: (1) Par example, il peut y avoir réduction de la densité de la plante nuisible visée, ce qui influe sur les sources d'alimentation de certains insectes parasites ou prédateurs. (2) L'agent biologique introduit pour la lutte contre la plante nuisible peut faire concurrence aux herbivores indigènes de la plant nuisible et les éloigner de leur aire naturelle, réduisant encore ainsi les sources de nourriture des ennemis naturels spécifiques de certains herbivores. (3) Toutefois, l'agent biologique introduit peut aussi servir de nourriture aux parasites et aux prédateurs des insectes nuisibles, ce qui pourrait favoriser la lutte biologique contre l'insecte nuisible, mais réduirait les effets de l'herbivore introduit sur la plante nuisible.

Le présent rapport donne des exemples des conflits mentionnés ci-dessus. Il donne aussi des directives pour éviter de réduire l'efficacité globale des agents biologiques de lutte contre les plantes nuisibles et les insectes. Les spécialistes en matière de lutte biologique doivent bien comprendre les relations multitrophiques dont ils doivent tenir compte dans les systèmes particuliers qu'ils étudient. Les chercheurs qui s'intéressent aux plantes nuisibles doivent accorder une attention particulère aux ennemis naturels des herbivores cibles, et les entomologistes, à leur tour, doivent analyser les effets des insectes parasites et prédateurs introduits sur les herbivores constituant des candidats potentiels pour la lutte biologique contre les plantes nuisibles.

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Biocontrol of Canada Thistle with Pathogenic Fungi

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Abstract

In Denmark, Canada thistle is attacked by several pathogens. Among them is the necrotrophic fungus, *Phomopsis cirsii*, which causes die-back of young as well as more mature thistle shoots. A survey of the fungus and investigations to assess its potential as a mycoherbicide against Canada thistle were begun at The Royal Veterinary and Agricultural University in Copenhagen in January 1983.

Greenhouse and laboratory tests have shown that the fungus posseses a high degree of specificity and pathogenity. This summer, different methods for field inoculations are under investigation. The effectiveness of inoculum prepared from different fungal structures is also being studied.

Further work concerns *Septoria cirsii*, a leaf-spot fungus causing defoliation of Canada thistle. Interactions between this pathogen and *P. cirsii* are under investigation.

Lutte Biologique Contre le Chardon des Champs par l'Introduction de Champignons Pathogènes

Au Danemark, le chardon des champs est atteint par plusieurs agents pathogènes. Parmi ceux-ci, mentionnons le champignon nécrotrophe, *Phomopsis cirsii*, qui provoque le dépérissement terminal des jeunes pousses et des pousses plus matures des chardons. L'étude de ce champignon et l'évaluation de son potentiel comme 'mycoherbicide' contre le chardon des champs ont été amorcées par l'Ecole royale vétérinaire et agronomique, à Copenhague, en janvier 1983.

D'après les essais en serre et en laboratoire, le champignon est extrêmement sélectif et pathogène. Cet été, on étudie diverses méthodes d'inoculation sur le terrain ainsi que l'efficacité des inoculations préparées à partir des différentes structures du champignon.

Les chercheurs s'intéressent aussi à un autre champignon, *Septoria cirsii*, qui provoque la tache des feuilles et, par conséquent, la défoliation des chardons des champs. On étudie actuellement les interactions entre cet agent pathogène et *P. cirsii*.

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Native Weeds as Candidates for Biological Control Research

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Abstract

More than 350 weeds in North America have been identified as causing major agricultural losses. Current control technology for most of these is not adequate. Some of these, including about 45 species of native weeds on rangelands, are being evaluated as potential candidates for biological control research. This paper examines to a limited extent the ecological importance of these native weeds to help judge the appropriateness of biological control research with insects for their control. Among the weeds considered are ecological dominants such as mesquite, creosote, big sagebrush, junipers, oaks and other species which are important components of North American plant communities as defined by Kuchler. Some native plants in the genera to which these weed species belong are under review as endangered or threatened species. Most of these genera also contain species which have significant value as food for wildlife. The self-propagating, self-dispersing and persistence characteristics of introduced insects for biological control mean that once released, the levels of control they impart and the areas they ultimately occupy cannot be adequately predicted. The use of insects for biological control could spell significant irreversible reduction of weed species well beyond the situations and areas where they are deemed problematic. Management strategies and control methods which are site specific and less persistent may be more appropriate solutions to native plant problems than biological control. The use of insects for the control of native weeds without adequate compliance to research protocols could pose risks to our biotic resources which could, in turn, place the biological control approach itself in jeopardy.

Lutte Biologique Contre les Plantes Indigènes

Étant donné que les agents de lutte biologique se propagent et se dispersent d'eux-mêmes et qu'ils sont persistants, une fois introduits il est impossible de prévoir ni de contrôle leur degré d'efficacite, ni leur répartition finale. Le recours aux méthodes de lutte biologique peut entraîner une réduction marquée et irréversible des plantes cibles, même pour les cas ou les régions où elles ne posent pas de problèmes. Contrairement aux plantes nuisibles importées, les plantes indigènes ont une certain valeur en raison du fait qu'elles appartiennent à des communautés complexes dont les éléments ont évolué de façon parallèle. Parmi les plantes indigènes proposées en vue de la lutte biologique, il existe des éléments écologiques comme le mesquite, l'armoise tridentée et *Larrea tridentata* qui dominent les communautés naturelles d'une grande partie des terres de l'Amérique du Nord occidentale. Contrairement aux espèces importées, ces plantes et la majorité des autres plantes indigènes font problème, non pas parce qu'elles manquent d'ennemis naturels qui les restreignent, mais plutôt à cause des méthodes de pâturage employées et parce que les gens veulent utiliser plus à fond les terres sur lesquelles elles poussent. Il semble prudent d'examiner et d'éliminer les causes des problèmes provoqués par les plantes indigènes et, si l'on juge qu'une lutte est toujours nécessaire ou souhaitable, d'utiliser des techniques moins persistantes et davantage axées sur le site que les méthodes de lutte biologique.

The biological control of weeds approach introduces exotic phytophagous insects and plant diseases to attempt to reduce the abundance of weeds.* As of 1974, 55% of the projects had achieved substantial or complete control of the targeted weeds (DeBach 1974). Biological control has achieved significant success against diverse weed types growing in many different environments including: musk thistle, *Carduus thoermeri* Weinmann (Compositae), a weed of range and pastures in the U.S. (Kok and Surles 1975; Rees 1977); skeletonweed, *Chondrilla juncea* L. (Compositae), a weed of wheat in Australia (Cullen 1978); and the floating fern, *Salvinia molesta* D.S. Mitchell (Salviniaceae), a problem in Australian lakes (Room *et al.* 1981) and Papua New Guinean waters (Thomas and Room 1985).

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*This exotic organism-introducing type of biological control is often referred to as 'classical' biological control. It is the traditional and most common form of biological control. Many other control techniques which rely on biotic components, such as fostering indigenous natural enemies or using competitive plants are also called biological control. This paper deals only with classical biological control.

Thus far, the biological control of weeds with insects has been used almost exclusively against naturalized weeds. The use of the introduced scale *Dactylopius opuntiae* Ckll. (Homoptera: Dactylopiidae), to control prickly pear cacti, *Opuntia* spp. (Cactaceae), on Santa Cruz Island, California (Goeden *et al.* 1967), is the only instance in North America where classical biological control has been used against native weeds. Native weeds have not been the target of biological control programs in the past because: (1) they are thought to already possess regulating natural enemies; (2) they are thought to be problematic primarily because of management practices, such as overgrazing; and (3) there are conflicts of interests over the value of the native weeds and their close relatives. Recently there has been increased interest in introducing biological control agents against native weeds in North America. DeLoach (1981) discussed this issue and recommended the use of biological control against some native plants, which are problem weeds of southwestern U.S. rangelands.

In 1983 a selective survey by United States Department of Agriculture weed scientists and biological weed control specialists identified > 350 weeds that caused severe losses in U.S. agricultural production. Current control technology is not adequate for many of these weeds. In the rangeland portion of the survey, 45 native North American weeds were identified for evaluation as candidates for biological control. Three weeds, *Gutierrezia* spp. (Compositae), *Larrea tridentata* (DC.) Coville (Zygophyllaceae), and *Rhus* spp. (Anacardiaceae), from the list of 45 were selected for biological control research. None of these 45 species have been targeted for biological control operations. While it appears to be technologically feasible to find natural enemies of the foreign relatives of our native weeds and to introduce these organisms against native weeds to reduce their abundance, the ecological ramifications of such introductions are not always fully understood. This paper examines to a limited extent the ecological importance of the native weeds identified in the survey, to help judge the appropriateness of using biological control methods against them.

The self-propagating, self-dispersing and persistence characteristics of introduced insects for biological control of weeds contribute significantly to the control they exert and to the economic advantages of the approach. These characteristics also mean that once the organisms are released the levels of control they impart and the areas they ultimately occupy cannot be adequately predicted. The use of insects for biological control can spell significant irreversible reduction of the targeted weeds beyond the situations and regions where they are considered problems. Native plants have ecological value and their reduction by biological control to lower levels than intended and beyond the areas where they are deemed problematic could be undesirable.

Among the native weeds being evaluated as candidates for biological control research are some ecological dominants such as mesquite, *Prosopis* spp. (Leguminosae); creosote bush, *L. tridentata*; big sagebrush, *Artemisia tridentata* Nutt. (Compositae); junipers, *Juniperus* spp. (Cupressaceae); and oaks, *Quercus* spp. (Fagaceae). These species define plant communities which occupy much of the land area of North America. Significant reduction of these species and others which have community importance could lead to destabilizations of their communities, the eventual loss of biotic resources and other unknown environmental effects. To obtain a measure of the plant community importance of the native species (and their congeneric close relatives which could possibly also be affected to varying degrees by biological control agents) Kuchler's (1964) manual of the potential natural vegetation of the continental United States was utilized. In this work he defines 116 vegetation types, naming a few dominant species and major components for each. Table 1 lists the numbers of species, for each of the genera containing the identified native weed species, which Kuchler defines as dominants and major components in the various communities. Some of the native species such as creosote bush (*L. tridentata*), which is listed as a dominant of six communities and a major component of another, and groups such as the sagebrushes (*Artemisia* spp.), which have three species listed as dominants in six communities and 12 species as major components in 17 communities, have significant position in the plant communities they define. Other identified species, particularly smaller herbaceous species and groups such as *Astragalus wootonii* Sheld. (Leguminosae) and *Ranunculus* spp. (Ranunculaceae), which contribute much less to plant community physiognomy, are unlisted by Kuchler. A total of 19 of the 32 genera, which contain the identified native weeds, have species listed by Kuchler as important components of North American plant communities.

Another indicator of a plant's ecological value is the number and types of interactions which they exhibit with other organisms, particularly those which are directly dependent upon it such as herbivores. Martin *et al.* (1951) provides a simple and convenient way to assess the value of the more important food plants of terrestrial vertebrates in the U.S. Their index of use for each plant genus is a ratio made up of the aggregate of the degrees of use of individual plant species used by each animal user species divided by the total number of animal user species. A low numerator over a large denominator indicates that the plant or plant group is used by many wildlife species but only to a limited extent by each. A higher numerator and small denominator characterizes a plant or group of great importance to a limited number of animals. The oak (*Quercus*) ratio is 263/96, which indicates high degree of use of many oaks by 96 animal species. Twenty of the thirty-two genera to which the identified native weed species belong, are recorded as food sources by Martin *et al.* (1951). The ratios of use for these plants are recorded in Table 1. Although useful, this index deals only with interactions of larger animals and plants. The full complement of associations which plants have with other organisms is, at best, imperfectly known.

Many of these native weeds and groups belong to genera which have large numbers of native species. This increases the numbers of non-target plants that could be affected by introduced biological control agents, which frequently have generic or subgeneric food plant host-specificity levels. Some of the larger genera to which the weedy native species belong are *Astragalus* with 333 spp., *Lupinus* (Leguminosae) with 146 spp., *Quercus* and *Ranunculus* with 76 spp., *Delphinium* (Ranunculaceae) with 67 spp., and *Artemisia* with 52 spp. (USDA, Soil Conservation Service 1982).

These large genera also greatly increase the chances that rare plants, which are currently under review for Federal protection as endangered or threatened species, could be potential non-target hosts for biological control agents introduced against their native weed relatives. The numbers of rare species currently under review in each genus, to which the identified native weed species belong, are listed in Table 1. There are 79 *Astragalus* spp., 26 *Lupinus* spp., 10 *Delphinium* spp. under review (USDI, Fish and Wildlife Service 1980, 1983). In all, 19 of the 32 genera, to which the identified species belong, have species under review.

Table 1. Characteristics of North American native weeds which are being evaluated as candidates for biological control research.

Candidate weeds being evaluated for biological control research	Common name	Habit	No. of North American species in the genus (North of Mexico)	No. of species in the genus under review for legally protected, endangered or threatened status	Plant community significance (Kuchler 1964)	Wildlife use index for the genera (Martin *et al.* 1951)
Acacia farnesiana (L.) Willd. (Leguminosae)	huisache	tree	18 S–T[1]	0	One *Acacia* sp. dominant in 1 community. Five *Acacia* spp. are major components in 9 communities.	7 plant species uses 7 wildlife species
Aloysia gratissima (Gilles & Hook) Troncoso (= *A. lycioides* Cham., *A. ligustrina*) (Verbenaceae)	whitebush	shrub	3 S	0	Not mentioned.	Not mentioned.
Artemisia frigida Willd. (Compositae)	fringed sagebrush	shrub	52 AP S	5	A major component in 6 communities.	
A. tridentata Nutl.	big sage-brush	shrub			A dominant in 4 communities and a major component in 3 communities. Nine *Artemisia* spp. are dominants in 5 communities and major components in 17 communities.	40/22
Astragalus emoryanus (Rydb.) Cory (Leguminosae)	locoweed	annual–biennial herb	333 ABP S	79	Two *Astragalus* spp. are major components in 3 communities.	9/10
A. mollissimus Torr.	locoweed	perennial herb				
A. wootonii Sheldon	locoweed	annual–biennial herb				
Baccharis glutinosa Pers. (Compositae)	baccharis	shrub	20 AP	2	A major component in 1 community.	1/1
B. halimifolia L.	baccharis	shrub			A major component in 1 community.	
B. neglecta Britton	baccharis	shrub			Four *Baccharis* spp. are major components in 3 communities.	

Brunnichia cirrhose **Gaertn. (Polygonaceae)**	redvine	woody vine	1		0	Not mentioned.	Not mentioned.
Campis radicans **(L.) Seem. (Bignoniaceae)**	trumpet creeper	woody vine	1		0	A major component of 1 community.	Not mentioned.
Crataegus **spp. (Rosaceae)**	hawthorns	trees and shrubs	37		3	Not mentioned.	22/29
Cuscuta **spp. (Convolvulaceae)**	dodders	parasitic vines	44	AP	2	Not mentioned.	Not mentioned.
Delphinium barbeyi **Huth. (Ranunculaceae)**	tall larkspur	perrenial herb	67	PH	10	Not mentioned.	Not mentioned.
Diospyros virginiana **L. (Ebenaceae)**	eastern persimmon	tree	2	ST	0	A major component in 1 community.	28/19
Eupatorium capillifolium **(Lam.) Small (Compositae)**	dog fennel	perennial herb	27	PH	5	Not mentioned.	3/2
Flourensia cernua **DC. (Compositae)**	tarbush	shrub	1		0	A dominant in 2 communities.	Not mentioned.
Gutierrezia microcephala **(DC.) Gray (Compositae)**	broomweed	shrub	10	AP	1	Two *Gutierrezia* spp. are major components of 5 communities.	14/9
G. sarothrae **(Pursh.) Britt. & Rusby**	broom snakeweed	shrub				A major component in 3 communities.	
Helenium amarum **(Rafin.) H. Rock (Compositae)**	bitter sneezeweed	annual herb	18	AP	0	Not mentioned.	Not mentioned.
Heterotheca subaxillaris **(Lam.) Britt. & Rusby (Compositae)**	camphorweed	annual herb	38	AP	4	Not mentioned.	Not mentioned.
Hymenoxys odorata **DC. (Compositae)**	bitterweed	annual herb	10	AP	4	Not mentioned.	Not mentioned.
H. richardsonii **(Hook.) Cockll.**	bitterweed	perennial herb				Not mentioned.	Not mentioned.
Ipomoea pandurata **(L.) G.F.W. Mey.**	bigroot morningglory	perennial vine	31	AP	2	Two *Ipomoea* spp. are major components of 1 community.	

Table 1. (Continued.)

Candidate weeds being evaluated for biological control research	Common name	Habit	No. of North American species in the genus (North of Mexico)	No. of species in the genus under review for legally protected, endangered or threatened status	Plant community significance (Kuchler 1964)	Wildlife use index for the genera (Martin *et al.* 1951)
Iva axillaris **Pursh. (Compositae)**	poverty weed	herb	13 AP	0	*I. fructescens* is a major component in 1 community.	Not mentioned.
Juniperus ashei **J. Buchholz (Cupressaceae)**		shrub-tree	14 ST	0	A dominant in 1 community.	66/44
J. monosperma **(Engelm.) Sarg.**		shrub-tree			A dominant in 2 communities.	
J. pinchottii **Sudw.**		shrub-tree			A major component in 3 communities.	
J. virginiana **L.**		tree			A dominant in 2 communities and a major component in 2 other communities.	
J. osteospermum **(Torr.) Little**		tree			Nine *Juniperus* spp. are dominants in 6 communities and 9 *Juniperus* spp. are major components in 8 communities.	
Larrea tridentata **(DC.) Coville (Zygophyllaceae)**	creosote bush	shrub	1	0	A dominant in 6 communities and major component in another.	8/4
Lupinus **spp. (Leguminosae)**	lupines	herbs and shrubs	146 AP	26	Five *Lupinus* spp. are major components in 8 communities.	19/13
Opuntia **spp. (Cactaceae)**	prickly pear cactii and cholla	perennial succulents	46	8	Two *Opuntia* spp. are dominant in 1 community and 8 *Opuntia* spp. are major components of 10 communities.	62/44
Parkinsonia aculeata **L. (Leguminosae)**	retama	tree	4 ST	0	Not mentioned.	Not mentioned.
Proboscidea louisiana **(Mill.) Thell. (Martyniaceae)**	devil's claw	annual herb	7 AP	1	Not mentioned.	Not mentioned.

Prosopis glandulosa Torr. (Leguminosae)	mesquite	shrub–tree	4 ST	0	A dominant in 6 communities and a major component in 2 communities.	52/24
P. velutina Wooton	mesquite	shrub–tree			A dominant in 1 community and a major component in 2 communities. Three *Prosopis* spp. are dominants in 7 communities and 4 *Prosopis* spp. are major components in 6 communities.	
Quercus spp. (Fagaceae)	oaks	shrubs and trees	76	4	Twenty-two *Quercus* spp. are dominants in 22 communities and 36 *Quercus* spp. are major components in 26 communities.	263/96
Ranunculus spp. (Ranunculaceae)	buttercups	herbs	76 AP	3	Not mentioned.	4/21
Salix spp. (Salicaceae)	willows	shrubs and trees	84	2	One *Salix* sp. is dominant in 1 community and 9 *Salix* spp. are major components in 9 communities.	37/25
Solanum carolinense L. (Solanaceae)	horsenettle	shrub	34 AP	2	Not mentioned.	17/45
S. elaeagnifolium Cav.	silver leaf nightshade	annual herb				
Toxicodendron radicans (L.) Kuntze (= ***Rhus radicans*** L., ***R. toxicodendron*** L.) (Anacardiaceae)	poison oak and poison ivy	vines and shrubs	5 PSV	0	A major component of 2 communities.	66/61
Ulmus alata Michx. (Ulmaceae)	winged elm	tree	7 T	0	A dominant in 1 community and a major component in another. Two *Ulmus* spp. are dominants in 4 communities and 4 *Ulmus* spp. are major components in 10 communities.	17/20

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[1] Habit Codes: A = annual; B = biennial; H = herb; P = perennial; S = shrub; T = tree; W = woody; V = vine.

The legal ramifications of releasing biological control agents which could impact and impair endangered plants and ecological dominants could be significant enough to severely damage the practice of the biological control approach.

Some of the identified native weed species are problems because of grazing practices and the desire on the part of people to use their land more totally. Before 1858, mesquite (*Prosopis glandulosa* Torrey) occupied only about 5% of the southern New Mexico range. By 1963, after the area was settled and intensive grazing had reduce the grass cover, over 50% of this range was occupied by mesquite (Klingman 1970). It seems desirable to examine and, if possible, correct the causes for native plants becoming weed problems. If control of a native weed is still needed or desired, then control strategies and technologies which are less persistent and more site specific than biological control may be more appropriate.

As previously mentioned, classical biological control research with insects has, to date, almost completely been restricted to naturalized weeds. To depart from this traditional orientation and begin research on biological control of native weeds may, in my opinion, prove to be an inappropriate research approach. Native plants often have value as parts of complex co-evolved communities. These communities are, in turn, the relatively stable and dramatic units that are, and which house, some of the rich biotic basis of our country. To begin research on biological control of native weeds could pose risks to both this biotic basis and to the biological control approach itself.

Biological control of weeds, like most technologies, has appropriate and inappropriate uses. The recognition of reasonable limits of application for the approach should improve and protect what has become a valuable method of weed management.

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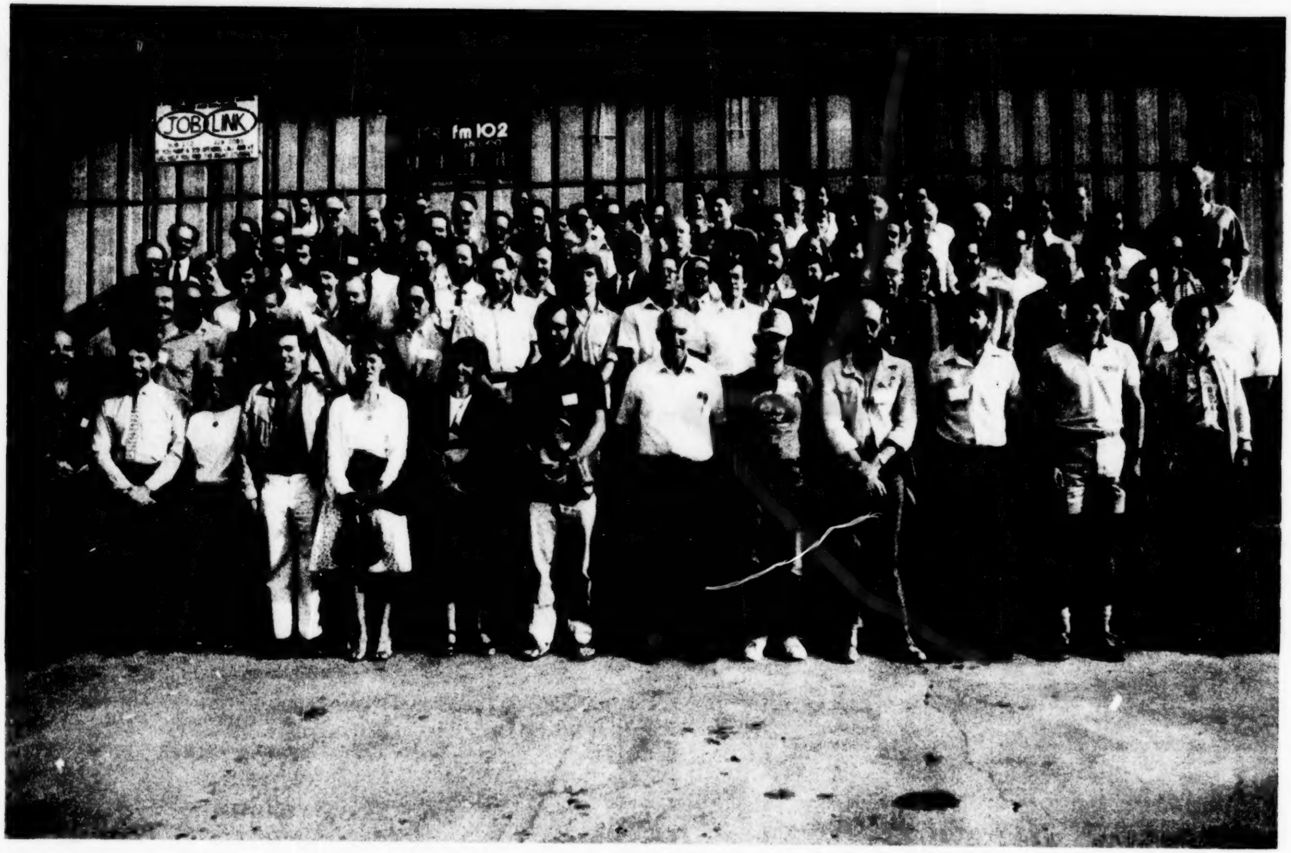
JOB LINK
fm 102

Key to Group Photograph, VI International Symposium on Biological Control of Weeds, 25 August 1984, University of British Columbia, Canada

Bottom Row:

1, E.S. Delfosse, **2**, R.W. Pemberton, **3**, S.S. Rosenthal, **4**, D.P.A. Sands, **5**, M.C. Fowler, **6**, M. Redfern, **7**, P.B. McEvoy, **8**, H.B. Johnson, **9**, J.P. Cuda, **10**, J. Gillett, **11**, W. Woods, **12**, N. Poritz, **13**, J.T. Yorinori.

Second Row:

14, P.M. Room, **15**, Y.H. Fayad, **16**, R. Kassulke, **17**, K.L.S. Harley, **18**, J.P. McCaffrey, **19**, G. Buckingham, **20**, N.A. Straw, **21**, R.E. Boldt, **22**, C.J. DeLoach, **23**, H.A. Cordo, **24**, J.F. Alex, **25**, J.K. Scott, **26**, H.J. Schoonbee, **27**, A.K. Watson, **28**, E. Bruzzese.

Third Row:

29, D.J. Politis, **30**, J. Medd, **31**, L. Wymore, **32**, M. Clement, **33**, S. Neser, **34**, R.P. Field, **35**, R. Charudattan, **36**, M. El-Wakil, **37**, G. Défago, **38**, R.E. Wall, **39**, F.X. Schubiger, **40**, J.M. Cullen, **41**, P. Syrett, **42**, G.P. Markin, **43**, G. Alber, **44**, M. Dunn.

Fourth Row: (Approximately)

45, K. Mortensen, **46**, R.W. Medd, **47**, P.C. Scheepens, **48**, S. Hasan, **49**, T.D. Center, **50**, E.E. Trujillo, **51**, A. McCain, **52**, J.R. Hosking, **53**, L. Anderson.

Fifth Row: (Sort of)

54, P.H. Dunn, **55**, C. Garcia, **56**, A.S. McClay, **57**, R.M. Nowerski, **58**, R. Lavigne, **59**, G. Anderson, **60**, R.E. Brown, **61**, J.M. Story, **62**, G.L. Piper, **63**, V. Leth, **64**, N.H. Sorensen, **65**, R. Hawkes, **66**, S. Forsyth, **67**, P.W. Mueller, **68**, R. Makowski, **69**, B.W. Willson, **70**, L. Littlefield, **71**, J.Wenz.

Top Row: (Use your imagination)

72, J.K. Balciunas, **73**, N.R. Spencer, **74**, F.D. Bennett, **75**, D. Schroeder, **76**, R.D. Goeden, **77**, H. Zwölfer, **78**, D.M. Supkoff, **79**, D. Gardner, **80**, E. Stutz, **81**, C.D. Hunter, **82**, A. El-Heneidy, **83**, P. Harris, **84**, D.B. Joley, **85**, M. Maw, **86**, C. Turner, **87**, R. Lalonde, **88**, D.T. Briese, **89**, W. Bruckart, **90**, L.A. Andres.